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EARLY ORDOVICIAN CONODONTS FROM THE BARRANDIAN AND BOHEMIAN-BALTIC FAUNAL RELATIONSHIPS

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The typical Baltic conodont *Baltoniodus* has been identified in the Bohemian Early Ordovician Klabavian and Sarkan stages. In the upper part of the Klabava Formation (locality Svatoštěpánský rýbnik near Mýto) *Baltoniodus* is associated with species of the genera *Drepanoistodus*, *Scalpellodus* and *Drepanodus*, which also occur in the Baltic area. This contrasts with dissimilarity, stressed by many authors, between Baltic and Bohemian faunas thought to belong to different paleozoogeographic provinces. A review of other groups of fossils indicates that migrations between these regions in the Early Ordovician were not uncommon. Klabavian *B. bohemicus* sp. n. is morphologically intermediate between *Acodus deltatus*, *B. crassulus*, and *B. triangularis sensu* Lindström, 1971 and may be identical with the oldest populations of *B. navis sensu* Van Wamel, 1974. According to the interpretation presented of the evolutionary relationships of *B. bohemicus* sp. n., the upper part of the Klabava Formation is correlated with the Latorpian--Volkhovian boundary. The conodontophorid assemblage from Mýto differs in its much lower diversity from Baltic assemblages containing species of the same genera. This supports the concept of the cold-water nature of the Bohemian Ordovician. It is suggested that the subpolar ("Antarctic") convergence was between Baltica and the Moldanubicum, and selectively separated faunas in the Early Ordovician.

Key words: conodonts, biogeography, Baltic region, Bohemia, Ordovician, evolution, biostratigraphy.

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INTRODUCTION

Together with the Baltic Region and the North American Midcontinent, the Barrandian basin is one of the occurrences of the Ordovician in the world that is most accurately described, richest in fossils and most complete. Despite the high diversity of fossils and their excellent state of preservation (review: Havliček and Vaněk 1966), the age correlation of the formations of the Bohemian Ordovician with other Ordovician deposits is very difficult due to considerable dissimilarity of faunas.

In considerations of the paleobiogeography of the European Ordovician, the Baltic Region has been contrasted traditionally with Ordovician localities, situated south of the Hercynids which have been connected together to form the Mediterranean Province, which also includes Bohemia (i.a. Marek 1976; Havliček 1976; Havliček and Branisa 1980). Due to troubles with an accurate age correlation between Bohemian lithostratigraphic units and British or Baltic stages, regional Ordovician stages have been designated in Bohemia (Havliček and Marek 1973; Přibyl 1979).

Differences between Baltic and Bohemian Ordovician localities are considered to be a result of the paleogeographic pre-drift configuration of the continental blocks to which they are assigned (Havliček 1976; Dzik 1978). Acceptance of this concept opens new possibilities for paleozoogeographic interpretation of evolution in faunas of particular regions. In studies thus directed zoogeographic and biostratigraphic aspects are inseparable, for it is necessary to know which of the faunas compared are coeval. At the same time, a determination of the sources of evolutionary separation and migration of species becomes the only chance to determine the age of faunas that are quite different in specific composition. The present paper is an attempt at correlating the Lower Ordovician lithostratigraphic units of Bohemia with those of the thus far most accurately studied Baltic division based on the conodonts. The interpretation of relationships in time between the Bohemian and Baltic conodonts is presented below against the background of relationships and dissimilarities of other faunal groups occurring in these regions.

MATERIALS

Conodonts on which the present paper has been based come from three outcrops: (1) Mýto, (2) Ejpovice and (3) Osek.

(1) Of the localities studied, conodonts are the most abundant in the environs of the town Mýto on the northern side of the Praha-Plzeň railroad line near the western margin of the Svatoštěpánský rýbnik (pond) (pl. 2: 1). It is an abandoned quarry now overgrown with shrubs. A diabase sill within clayey shales crops out at the bottom of the quarry. Near the sill, the shale is thermally metamorphosed. A 27 cm thick intercalation of limy tuffite (pl. 2: 2; fig. 1) occurs in shales about 190 cm above the sill. A diagonal lamination of shale is visible just below the intercalation. A similar, but fine-grained calcareous tuffite also crops out above the pond in a road that intersects the railroad track (pl. 2: 2). Dark shales with Šarka Formation concretions crop out in the bank of the pond some meters above the tuffite intercalation. The contact between the Klabava and Šarka formations is invisible. Conodonts were discovered by Dr. Ladislav Marek (Geologický ústav ČSAV, Prague) on

fractured rock surfaces. In 1977, during my stay in Prague, he showed me this outcrop and assisted my sampling.

The calcareous tuffite of Mýto contains an abundant and well preserved fauna, which is now being studied by Dr. Michael Mergl of the Karlova Universita, Prague (macrofauna) and Dr. Miroslav Krůta of the
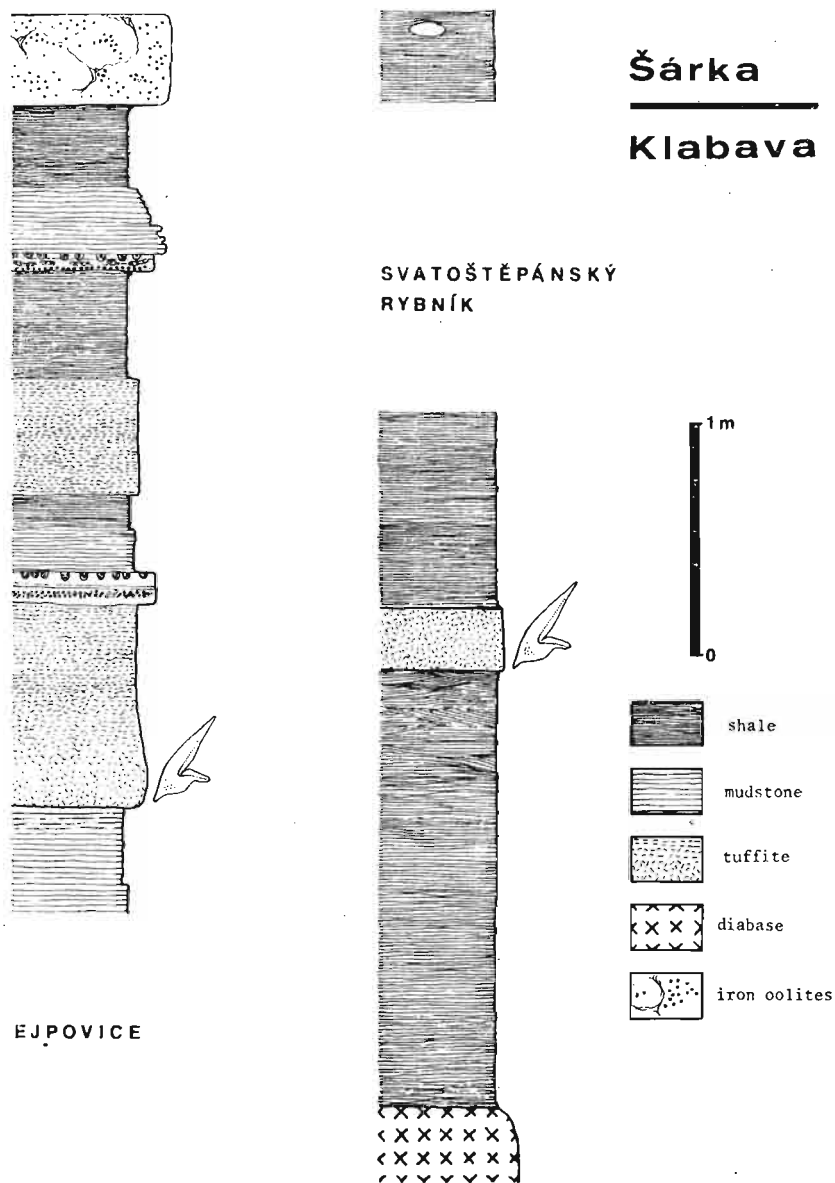

Fig. 1. Geological section of the uppermost parts of the Klabava Formation at the localities Ejpovice (old iron mine; see pl. 1: 1—2, 6: 1—2) and Svatoštěpánský rýbnik near Mýto (abandoned quarry; see pl. 2: 1—2). Indicated fossiliferous layers of calcareous tuffite.

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Ústřední geologický ústav, Prague (ostracods). Previously published data on graptolites, occurring in clayey shales of this outcrop, include *Tetragraptus* cf. *bigsbyi* (Hall, 1895), *T. reclinatus abbreviatus* Bouček, 1956 (= *T.* cf. *pseudobigsbyi* Skevington, 1965 of Kraft 1977) and *Azygograptus* sp. (Bouček 1973; Kraft 1977). The beds of Mýto, based on these graptolites, are included in the *T. abbreviatus* Zone of the local Bohemian division. The residue contains numerous spiculae of siliceous sponges, which have probably been secondarily calcified (pl. 5: 5—7), although there are some arguments for an originally calcareous structure of similar forms from the Baltic Ordovician (Lindström 1979). Several species of ostracods (fig. 6) and acrotretid brachiopods occur subordinately.

(2) The contact between the Klabava and Šarka formations crops out in an abandoned iron-ore mine at Ejpovice (pl. 1: 1—2). A transition from the clayey shales and calcareous tuffites of the Klabava Formation to the pelosiderites and iron oolites of the Šarka Formation is visible at the outlet of the river channel. Blue-gray tuffites, which crop out near the top of the Klabava Formation, abound in the detritus of orthid brachiopods. The tuffites resemble in color those of Mýto, but are softer and are pale colored. The conodonts they contain are few and poorly preserved. Above the tuffites are thin ferruginous intercalations in dark-red clayey shales with shallow, round borings filled with iron oolites (pl. 6: 2). Tonguelike trace-fossils occur in a red shale between these intercalations (pl. 6: 1).

Through the courtesy of Dr. Marek, I had an opportunity to acquaint myself with, and to sample, the Ejpovice outcrop in 1980.

Many borings were made at Ejpovice during preparation for the exploitation of the iron ore. Part of the material from these borings has been elaborated paleontologically but considerable faulting of the layers prevented an accurate comparison of data. According to Bouček (1973), the graptolites *Schizograptus tardibrachiatus* Bouček, 1973, *Expansograptus extensus* (Hall, 1865), *Acrograptus nicholsoni* (Lapworth, 1875), *Didymograptus protobifidoides* Bouček, 1973 and *Azygograptus suecicus* Moberg, 1892, which represent various horizons of the Arenigian, occur in the Klabava Formation.

A detritus of orthid brachiopods, calcified (?) spiculae of siliceous sponges (of the *Calcihexactinia* type) and fragmentary elements of *Drepanodus* sp. and *Drepanoistodus* sp. are contained in the residue.

(3) Siliceous concretions, called in Czech "rokycanské kuličky", collected in the fields of the village Osek near Beroun, were turned over to me by Dr. Pavel Šlehofr (Geologický ústav ČSAV). These concretions, occur as washed out from shales of the Šarka Formation (L. Marek, oral communication). The graptolites they contain are indicative of the *Corymbograptus retroflexus* Zone (Bouček 1973). Most Lower Ordovician fossils of Bohemia known in the literature, including numerous trilo-

bites, crustaceans, mollusks and carpoids (cf. Havliček and Vaněk 1966) come from these concretions. Many Chitinozoa, sphaeromorphs, spiculae of siliceous (?) sponges (secondarily calcified?), acrotretids, brachiopods, plates of carpoids, larvae of gastropods and plates of machaeridians were contained in a residue obtained by dissolving about 0.5 kg of the concretions. I have also found a few elements of *Baltoniodus*.

METHODS

The calcareous tuffites of Mýto and Ejpovice were dissolved alternately in formic and hydrofluoric acids. The rock, crushed into fragments about 2 cm in diameter, was decalcified in 20 per cent HCOOH to the cessation of reaction, that is, for about 48 hours. After washing, the rock was covered with concentrated H_2F_2 for 15 minutes and, subsequently, the residue was washed. After treating the residue repeatedly with hydrofluoric acid, when an excess of calcium fluoride appeared in the residue, the decalcification was repeated in formic acid.

The "rokyčanské kuličky" of the Šarka Formation dissolve excellently in hydrofluoric acid.

PALEOGEOGRAPHY OF THE EARLY ORDOVICIAN

Paleomagnetic and paleoclimatic data enable a moderately unequivocal interpretation of the situation of the main Ordovician continental plates in relation to the equator and the poles (Ross 1976; Havliček 1976; McTavish and Legg 1976; Bergström 1979; Scotese et al. 1979; Ziegler et al. 1979). It is more difficult, however, to indicate the relation between the main plates and smaller ones that contain epicontinental deposits with the fauna discussed below, for example, the Holy Cross (Świętokrzyskie) Mountains, the Sudeten Mts. and the Moldanubicum. On the basis of the character of sedimentation (an almost complete lack of limestones and reef-building organisms and considerable contribution of siderites — Havliček and Šnajdr 1955; Hirschmann et al. 1968; Kraft 1975), it is assumed that the Barrandian basin was situated during the Ordovician in the polar or subpolar climate zone, whereas the Baltic Region and the Holy Cross Mts (with their predominantly platform calcareous sedimentation, devoid of reef-building organisms and bioherms) were situated in the temperate climate zone (Spjeldnaes 1967; Havliček and Vaněk 1966; Havliček 1976; Sheehan 1979; Havliček and Branisa 1980). Such a situation of the Baltica continent (the East European Platform) is confirmed by paleomagnetic data, which indicate an about 30° distance from the South Pole (Bergström 1979). Palinspastic reconstructions of pre-Hercynian and pre-Caledonian Central Europe (Cwojdziński

1977, 1980; Dzik 1978a) place the Moldanubicum closer to the pole than
Baltica, assuming the orientation based on paleomagnetic data. The Holy
Cross and Sudeten Mountains, as well as the Moldanubicum were then
situated at a considerable, but now rather indeterminate, distance from
Baltica and were oriented perpendicularly to the Teysseire-Tornquist
line. According to the hypothetical situation of the pole close to the
African coast of Gondwana, these plates had to be situated between
Gondwana and Baltica (fig. 7).

COMMENTS ON UNITS IN MARINE PALEOBIOGEOGRAPHY

The need for an unequivocally understood, hierarchical classification
of paleobiogeographic units is very urgent (cf. Waterhouse 1976; Kauff-
mann and Scott 1976). Despite a considerable number of terminological
suggestions (cf. Sylvester-Bradley 1971), it is still a long way to the
uniformity of views in this domain. This results primarily from a limited
applicability to the biogeography of the oceans of classifications, based
on continental assemblages. As a rule, continental ecosystems have
discrete geographic borders that correspond to the sharply outlined
borders of continents or to the unequivocal separation of lowland areas
by mountain ridges, etc. Most marine biocoenoses are devoid of exter-
nal limits of this type. Discrete boundaries could result from a con-
siderable internal integration of biocoenoses and maybe also from the
related lack of continuous transitions between biocoenoses of various
types. The higher the rank of a biogeographical unit, however, the lower
is the degree of integration. At the level of an ecosystem corresponding
to a single biocoenosis (community) the degree of integration is very
low or almost none at all (Hoffman 1979). Continuity of spatial and struc-
tural transitions between biocoenoses of various types is well substant-
iated empirically (i.a. Cisne and Rabe 1977; Dzik 1979). The only excep-
tion are biocoenoses in which the concentration of biomass is so great
that it causes significant environmental changes. Biocoenoses of this
type have sharply outlined territorial boundaries. Here belong, for
example, reefs of various types, bioherms and banks (i.a. Dzik 1982b).

In 1976, Waterhouse proposed a hierarchical classification of biogeo-
graphic units based on the rank of taxonomic units characteristic of them.
The essential shortcoming of this system lies in its basic assumption,
because the ambiguity and instability of taxonomic ranks intensifies as
newer and newer "philosophies" of taxonomy are introduced. Thus, one
can be apprehensive for the uniformity and stability of understanding
biogeographic classifications based on them. A better way was chosen
by Kauffmann and Scott (1976) who suggested a hierarchically complex
classification of biogeographic units based on the percentage of endemic
taxa. However, introduction of such a quantification to descriptions of

Ordovician biogeographic units encounters serious methodologic difficulties, for the degree of endemism varies in particular groups of organisms (the similarity of conodont and dissimilarity of trilobite faunas, in Bohemia and in the Baltic Region, discussed below, may serve as an excellent example in this respect). Even with the assumption of an equivalent number of endemites, regardless of taxonomic group, this has to result in making the rank of a biogeographic unit dependent on the degree of a taxonomic elaboration of faunas. Such an assumption seems unacceptable since the concept of endemism of a nektonic cephalopod passing, in its development, the stage of a planktonic larva is different from that of, for example, a benthonic gastropod whose entire larval development takes place within egg capsule.

To avoid an ambiguous or arbitrary selection of detailed criteria of the classification, I adopt, for the purposes of the present paper, a simplified classification of biogeographic units, based not on postulated internal integration, but on external limits of the areas occupied by ecosystems and on analogies with territorial limits of continental ecosystems. In such a case, the possibility of determining objectively the boundaries is limited by the possibility of finding discrete boundaries in the zones of activity of these external factors. These may be seashores, a boundary of a continental shelf, a thermocline, a zone of convergence between warm and cold currents, a range of an uplift supplying biogens, etc.

Such biogeographic units can be treated as ecosystems, in this particular case having a somewhat higher rank than that traditionally employed (cf. Kauffmann and Scott 1976). The concept of ecosystem in ecology usually concerns a possibly small biocoenosis (community), together with its abiotic environment, which may function as a system that is closed with respect to the flow of biological information (that, is, functional information contained in living systems and made use of for controlling the flow of energy and matter between living and inanimate systems). An ecosystem is of course open to the flow of energy and matter, together with structural information contained in it. Thus, this is a system with a stable biological information content. Refuting the concept of an internally integrated discrete type of marine community (Hoffman 1979), induces one to seek an equivalent for continental ecosystems with the properties presented above (such as a forest, lake, etc.) at a higher level of organization of marine communities. The term ecosystem (as a system with an almost closed cycle of biological information) may be ascribed to the epicontinental sea limited by the margin of the shelf and to the shore of the continent separating it from adjacent seas. And this is the meaning of biogeographic unit that I adopt in this paper. The MacArthur and Wilson's (1963, 1967; see also Williams 1976) model of land biogeography may be applied to a marine ecosystem understood in this way.

In contrast to Recent marine ecosystems, studied by ecologists, the climactic fossil ecosystems have a significant time dimension. From its existence there follows the necessity of taking into account the flow of and changes in biological information content of fossil ecosystems. These changes are expressed in the following biogeographic processes:

(1) Evolution in particular species (debatable, however, is the integration of evolutionary processes within ecosystems, cf. Boucot 1975);

(2) Shift of communities within ecosystems (faunal shift, Jaanusson 1976);

(3) Migrations of species from other ecosystems, which may lead, in the scale of geological time, to changes in MacArthur and Wilson's (1963) faunal equilibrium.

There is a possibility of forming a hierarchical system of biogeographic units with a varying degree of informational "leakage". Two such units, with their meaning defined below, will be used in my further considerations:

(1) A province understood as an area of occurrence of marine communities between which a free flow of species occurs. The Ordovician epicontinental Baltic Sea or present-day North Sea may serve here as typical examples.

(2) A realm understood as an assemblage of provinces separated from each other by topographic barriers (for example, an ocean deep) which make faunal exchange difficult but not impossible. This assemblage is separated from others by hydrographic bariers emphasizing climatic differences and strongly limiting migrations (for example, boundaries of continents, convergences of marine currents, etc.). The Recent Antarctic region, separated by the Antarctic convergence, is a typical example in this respect.

SYSTEMATIC DESCRIPTIONS

NOMENCLATURE OF PARTICULAR ELEMENTS OF THE CONODONT APPARATUS

At present, at least five different systems of designating the types of elements of the conodont apparatus are employed in conodont literature (see Sweet 1981). They may be combined to form two groups: (1) a group in which the names of types of elements have been formed after the best known form-genera of conodonts; this system does not give any information on the mutual situation and number of elements and, if necessary, enables including by "intercalation" new types of elements; (2) a group of systems derived from the existence of that is known as a transition series and denoting elements of these series by consecutive letters or combinations of letters which implies a definite sequence and number of element types in an apparatus (Sweet and Schönlaub 1979; Sweet 1981).

Despite the opinion of Barnes et al. (1979), most conodonts had apparatuses of similar structure, as indicated by the possibility of homologizing the structure of apparatuses of ramiform elements from the Ordovician to the Triassic (Dzik and

Trammer 1980). Likewise. as shown by the few data on Ordovician natural assembla-
ges (clusters) of coniform elements (Nowlan 1979; Aldridge 1982), their structure
is similar. The existence of an apparatus with a secondarily reduced number of
elements (for example, in *Eoplacognathus* or *Complexodus*) or with elements secon-
darily resembling each other (for example, *Icriodus*) does not shake this view.
There are no practical and theoretical counterindications concerning the application
of the earliest and most widely employed classification by Jeppson, checked up
from the Ordovician (Dzik 1976) to the Triassic (Dzik and Trammer 1980). For
this reason, I also employ it in the present paper. An additional *ke* type of
elements is introduced for homologues of the keislognathiform element of *Amorpho-
gnathus*.

Suborder **Prioniodontina** Dzik, 1976

Remarks. — I included in this suborder (Dzik 1976) conodonts with an appa-
ratus marked by triramous *sp* and *oz* elements; a tetraramous (or four-ribbed)
pl elements is the most characteristic feature of typical representatives. I also
include here arbitrarily the Panderodontidae which, together with other forms
originally not having geniculate oistodontiform *ne* elements in their apparatus,
deserve to be separated in the future as an independent suborder.

Family **Panderodontidae** Lindström, 1970

Emended diagnosis. — Apparatus composed of coniform or serrated elements
with a deep basal cavity and characterized by low diversification of elements.
Relationships. — Panderodontidae differ from the Protopanderodontidae in
deep basal cavity of elements and from the remaining families of coniform cono-
donts, Distacodontidae and Oistodontidae, in that an *ne* element is not distin-
guishable morphologically. An element resembling, but not necessarily homologous
with the oistodontiform element of the Distacodontidae occurs only in *Belodina*.

Scalpellodus Dzik, 1976 *sensu* Löfgren, 1978

Type species: *Protopanderodus latus* Van Wamel, 1974.
Remarks. — In 1976 (Dzik 1976: 421) I considered Volkhovian populations of
S. latus to be conspecific with Lasnamägian populations, which I assigned to
S. cavus (Webers, 1966), which is based on materials from the Caradocian of
North America. Acknowledging *S. latus* as a later synonym of the latter, I ne-
vertheless indicated it as type species of *Scalpellodus*, because the structure of
its apparatus is much more accurately studied. As indicated by Löfgren (1978),
during the period between the Volkhovian and Aserian, *Scalpellodus* displays
evolutionary changes, which justify the separation of several temporal species
(perhaps, it would be better to give them the rank of temporal subspecies; cf.
Cooper 1981). In the development of a sharp edge on the posterior part of cusp of
some types of elements of the apparatus, populations of *Scalpellodus* from the
Lasnamägian seem to be even more advanced than the Aserian species *S. viruensis*
Löfgren, 1978, and they may be conspecific or at least closely related to the
American *S. cavus*.
As understood by Löfgren (1978), *Scalpellodus* includes forms related to *Pan-
derodus* whose elements differ in the lack of a lateral fissure. *Panderodus* is
probably a descendant of early representatives of *Scalpellodus*. A species with
a symmetric element with two lateral carinae in its apparatus (Cooper 1981: pl.

27: 9), which is unknown in the Baltic representatives of this genus, was assigned by Cooper (1981) to *S. latus*. It seems that this species belongs rather to *Semia-contiodus* and is related with *S. carinatus* Dzik, 1976.

Scalpellodus laevis Dzik, 1976
(pl. 2: 3—4; pl. 5: 5a, b)

1976. *Scalpellodus* (? *Cornuodus*) *laevis* Dzik: 421, fig. 13a—c; pl. 41: 1.
? 1978. *Cornuodus bergstroemi* Serpagli; Löfgren 51, pl. 4: 37, text-fig. 25D.
? 1978. *Cornuodus longibasis* (Lindström) *partim*; Löfgren 49—51, pl. 4: 36, 38 (*non* 39—42), text-fig. 25B (*non* A, C).

Material. — Nineteen specimens.

Description. — Elements of *S. laevis* identical with those illustrated by Dzik (1976) occur in the Klabava Formation. In addition to these elements, which have an oval, almost symmetrical transverse section at the level of the bend and a lenticulate transverse section in their distal parts (pl. 2: 4), there occur elements displaying a distinct keel on the entire posterior edge of the cusp (pl. 2: 3), as well as elements with a twisted axis (pl. 4: 5a). An expanded basal cavity is their common feature. Some elements have a smooth surface, but in others (pl. 4: 5b) the surface is delicately ribbed longitudinally.

Remarks. — The spectrum of element types presented above is typical of *Scalpellodus*. Ornamentation of the surface of some elements is also typical of its species (Löfgren 1978). I did not find elements with three ribs on the posterior margin, either in the sample from the Klabava Formation or in the Baltic erratics (Dzik 1976). Thus, Löfgren's (1978: 50) claim that *S. laevis* belongs to *Cornuodus longibasis* (Lindström, 1955), seems not to be justified. In Löfgren's materials, the ratio of elements of *C. longibasis* with three posterior ribs to asymmetric elements is 254: 58 and therefore, their lack in my material cannot be ascribed to small sample size. Aslo rather unlikely is the occurence in the Klabava Formation of a few elements of *C. longibasis* together with more numerous elements of some other species of *Scalpellodus*. None of the known species of this genus (except for *S. laevis* which is here included in it) has elements with such a strongly inflated base (cf. Löfgren 1978). I do not reject a possibility that *S. laevis* is conspecific with *C. longibasis* but I hesitate to use the latter name for the Bohemian population until diagnostic for the genus *Cornuodus* elements with three posterior ribs are found.

Distribution. — *P. originalis* Zone (Volkhovian) to *E. reclinatus* Zone (Lasnamä-gian) of the Baltic Region and Klabavian of Bohemia (Svatoštěpánský rýbnik near Mýto).

Drepanodus Pander, 1856

Type species: *Drepanodus arcuatus* Pander, 1856.

Drepanodus cf. *arcuatus* Pander, 1856
(pl. 3: 5—7)

1966. *Drepanodus* sp.; Špinar *et al.*: 986, fig, XIII—28.
1978. *Drepanodus arcuatus* Pander; Löfgren: 51, pl. 2: 1—8.

Material. — Twenty-two specimens.
Remarks. — Elements of this species from the Klabava Formation are not

different from Baltic ones. There occur both straight, drepanodontiform elements and "oistodontiform" ones that are strongly bent at the base of cusp. *Drepanodus* elements are hyaline, but, as a result of the preparation method here employed, they do not differ from elements of genera marked by the presence of white matter in the cusp. This precludes distinguishing some juvenile elements of *Drepanodus* from similar ones of *Drepanoistodus*.

This species differs from *Drepanodus franconicus* (Sannemann, 1955) from the Frankenwald in bending of cusp of "oistodontiform" element just above the basal cavity.

Distribution. — Supposedly worldwide (cf. Löfgren 1978). Klabavian of Bohemia: Svatoštěpánský rýbnik (calcareous tuffite), Ejpovice (calcarous tuffite) and Klabava (shales).

Family **Distacodontidae** Bassler, 1925

Emended diagnosis. — Conodonts with an apparatus of coniform elements; *ne* element with sharp margins and with an incision below the posterior margin (oisto-dontiform), *tr* element with a sharp anterior margin (suberectiform), and lateral processes that are lacking or very weakly developed.

Relationships. — Distacodontids differ from the closely related Oistodontidae in having *tr* elements without lateral processes.

Drepanoistodus Lindström, 1971

Type species: Oistodus forceps Lindström, 1955.

Drepanoistodus forceps (Lindström, 1955)?
(pl. 3: 1—4)

1974. *Drepanoistodus forceps* (Lindström); Van Wamel: 64—65, pl. 2: 14—22.
1976. *Drepanoistodus suberectus forceps* (Lindström); Dzik: 432, fig. 19a—k.
1978. *Drepanoistodus basiovalis* (Sergeeva); Löfgren: 55—56, fig. 26B—C, pl. 1: 11—17.
1978. *Drepanoistodus?* cf. *venustus* (Stauffer); Löfgren: 56—57, pl. 1: 7—8.
1978. *Drepanoistodus? venustus* (Stauffer)? Löfgren: 57, pl. 1: 9—10.
1979. *Drepanoistodus basiovalis* (Sergeeva, 1963); Bednarczyk: 424, pl. 4: 13—14.
1979. *Drepanoistodus forceps* (Lindström, 1955); Bednarczyk: 425, pl. 4: 8, 5: 7, pl. 7, 6: 12.

Material. — Drepanodontiform elements (*sp + oz + pl + hi*) — 47 specimens; *ne* — 18 specimens; *tr* (suberectiform) — 5 specimens.

Remarks. — Van Wamel (1974: 65) was the first to observe that "the oistodiform elements are highly variable. Forms described as *Oistodus basiovalis* Sergeeva occur together with forms described as *Oistodus forceps* Lindström and intermediate forms. From below upwards in the stratigraphic sequence, there is a gradual increase of the relative amount of *Oistodus basiovalis* forms per fauna." I also found a similar variability in the *ne* element from Baltic erratic boulders (Dzik 1976: 402).

To explain the occurrence of *ne* elements of the type of *Oistodus forceps* in samples displaying a predominance of *O. basiovalis*, Löfgren (1978) suggested the

occurrence of the species D.? *venustus*, independent of the D. *forceps* — D. *basio-
valis* group and having exclusively *ne* elements of the type of D. *forceps*. To
support her thesis, she mentioned changes in the proportions of the content of
drepanodontiform and oistodontiform (*ne*) elements in samples that she assigned
to D. *forceps* (older) and D. *basiovalis* (younger). Due to strongly varying hydro-
dynamic and mechanical properties of conodonts, I doubt if it is possible to re-
construct their original contribution to an apparatus on the basis of quantitative
data. Changes in the ratio of particular types of elements occurring in samples
may result from changes in the energy of the environment and not necessarily
from the composition of apparatus. Besides, changes described by Löfgren lie in
a decrease in the frequency of the *ne* element in subsequent samples and, therefore,
contrariwise to the idea of the formation of D.? *venustus*, a species having only *ne*
elements which should increase contribution of *ne* elements to samples. Löfgren
(1978: 56) also stated that D. *forceps* and D. *basiovalis* occurred together through
a certain extent of time. This is a result of treating these species typologically.
Otherwise, this should be interpreted either as a result of sympatric speciation
and extinction of the older species with a certain delay, or of allopatric speciation,
which involved formation of D. *basiovalis* elsewhere, extension of its range and
gradual displacement of D. *forceps* from its niche (cf. Dzik and Trammer 1980: 73).
I uphold my view that D. *forceps*, D. *basiovalis* and at least Baltic D. *suberectus* are
parts of one sequence of phyletic evolution. Differences between populations that
vary in age, which was the basis for separating these taxa, are so small that
differentiation, in particular of the first two species, needs detailed biometric studies
of large samples (see fig. 8).

The Mýto sample displays a predominance of *ne* elements of O. *basiovalis*
morphotype. According to Lindström (1971), O. *basiovalis* occurs only in BIIβ
(Middle Volkhovian), but for the reasons presented above I do not think that the
age of the Mýto sample can be deduced on this basis. North American D. *angu-
lensis* (Harris 1962) (see Ethington and Clark 1981) and Australian D. *pitjanti* Cooper,
1981, both of comparable age, have a *ne* element that is much more robust than
those from the Bohemian population.

Distribution. — Possibly worldwide (cf. Löfgren 1978); Early Ordovician be-
ginning with the Billingen substage. Klabavian of Bohemia: Svatoštěpánský rýbnik
near Mýto and Ejpovice.

Family **Balognathidae** Hass, 1959

Emended diagnosis. — Conodonts with a highly differentiated apparatus, includ-
ing an element *pl* with four processes (tetraprioniodontiform); *sp* (amorphognathi-
form) and originally a *ke* (keislognathiform) elements with three processes; a *ne*
(oistodontiform or falodontiform) element commonly with weakly denticulated pro-
cesses and an incision below the cusp.

Relationships. — Balognathids differ from the Prioniodontidae in having ty-
pically an apparatus with distinct *sp* and *oz* elements; from the Oistodontidae and
the early Ozarkodinina in having a tetraramous *pl* element (*Tetraprioniodus* vs.
Cladognathus form genera) and from the later Ozarkodinina in having a *ne* ele-
ment devoid of prominent denticles on the posterior process (*Falodus* vs. *Cyrtonio-
dus* form genera), except for late species of *Amorphognathus*.

Remarks. — If, as proposed below, denticulation formed independently in the
Acodus deltatus → *Prioniodus transistans* → *Prioniodus elegans* (type species of
Prioniodus) (cf. McTavish 1973) and A. *deltatus* → *Baltoniodus crassulus* vel B. *bo-*

hemicus sp. n. → *B. navis* (type species of *Baltoniodus*) (cf. Lindström 1971 and Van Wamel 1974) lineages, the family Prioniodontidae is polyphyletic. To avoid polyphyletism, *Acodus* Pander, 1856; *Tripodus* Bradshaw, 1969 (= *Diaphorodus* Kennedy, 1980), and *Eoneoprioniodus* Mound 1965 (= *Triangulodus* Van Wamel 1974 and *Trigonodus* Nieper, 1969) should be also included in this family or it should be divided into Prioniodontidae s. s. and Balognathidae (including *Baltoniodus*). In the last-named case, it appears difficult to present a practical diagnosis of these families due to a far advanced homeomorphy (?) of *Prioniodus* and *Baltoniodus*.

Genera assigned. — *Baltoniodus* Lindström, 1971, *Rhodesognathus* Bergström and Sweet, 1966, *Amorphognathus* Branson and Mehl, 1933, *Eoplacognathus* Hamar, 1966; *Polyplacognathus* Stauffer, 1935; *Complexodus* Dzik, 1976. Possibly also undenticulated *Acodus* Pander, 1856; *Tripodus* Bradshaw, 1969 (= *Diaphorodus* Kennedy, 1980), *Eoneoprioniodus* Mound, 1965 (= *Trigonodus* Nieper, 1969, *Triangulodus* Van Wamel, 1973) and *Stolodus* Lindström, 1971.

Baltoniodus Lindström, 1971

Type species: *Prioniodus navis* Lindström, 1955.

Remarks. — The type species of *Prioniodus* and *Baltoniodus* have almost identical apparatus structure and elements of very similar shape. For this reason, many authors have considered them to be subjective synonyms (Van Wamel 1974; Dzik 1976; Löfgren 1978). It is difficult to cite a character that would allow assignment of species unequivocally to these genera. According to McTavish (1973) and Lindström et al. (1974), the wide, gaping basal cavity of *Baltoniodus* elements is such a character. It seems, however, that such a shaped basal cavity is a primary feature inherited from *Acodus deltatus* and it need not necessarily indicate that elements displaying it belong to *Baltoniodus*. According to Lindström (1971) and Van Wamel (1974), *Baltoniodus navis* evolved from *A. deltatus*, independently of the *P. elegans* lineage. Analysis of the relationships of *B. bohemicus* sp. n. convinced me of the soundness of this view. Therefore, to avoid considering of a polyphyletic genus, I treat *Baltoniodus* as a separate genus. The only difference between *Prioniodus* and *Baltoniodus* is in higher diversification of the *sp* and *oz* elements in later species of *Baltoniodus*.

Baltoniodus bohemicus sp. n.
(fig. 2; pl. 2: 5, pl. 4: 1—4 and pl. 5: 1—4)

?1974. *Prioniodus navis* Lindström early form; Van Wamel: 89, pl. 8: 13, 15.

Holotype: *ne* element, ZPAL CXII/12; pl. 5: 4.
Diagnosis. — A species of *Baltoniodus* characterized by an undenticulated *ne* element with short processes; robust, undenticulated *sp* and *oz* elements, which are probably similar to each other, weakly denticulated *ke* element with a strong, undenticulated lateral process.
Material. — *oz* + *sp* + *ke* elements: 54 specimens; *pl*: 54 specimens; *hi*: 64 specimens; *ne*: 53 specimens; *tr*: 15 specimens.
Relationships. — *Baltoniodus bohemicus* sp. n. differs from *B. crassulus* (Lindström) *sensu* Van Wamel in having an *ne* element with a short posterior process:

from *B. navis* (Lindström, 1955) and *B. triangularis sensu* Lindström, 1971 in having
an *ne* element with a short, undenticulated anterior process; from *B. pseudoramis*
(Serpagli) (? including *Acodus gladiatus sensu* Serpagli, 1974) in having *ne* elements
in which both processes are short. Differences in the morphology of the remaining
types of elements are more difficult to determine due to a considerable variability.
Robust *sp* + *oz* elements distinguish *B. bohemicus* from all the species mentioned
above except *B. triangularis sensu* Lindström, 1971, which, however, has a more
distinct denticulation and discernible *sp* (with a large angle between processes) and
oz (shaped like a tall pyramid) types. *B. bohemicus* also differs from *P. transistans*
McTavish, 1973, which is in the same stage of denticulation development, in
undenticulated or very indistinctly denticulated *sp* and *oz* elements and a distinctly
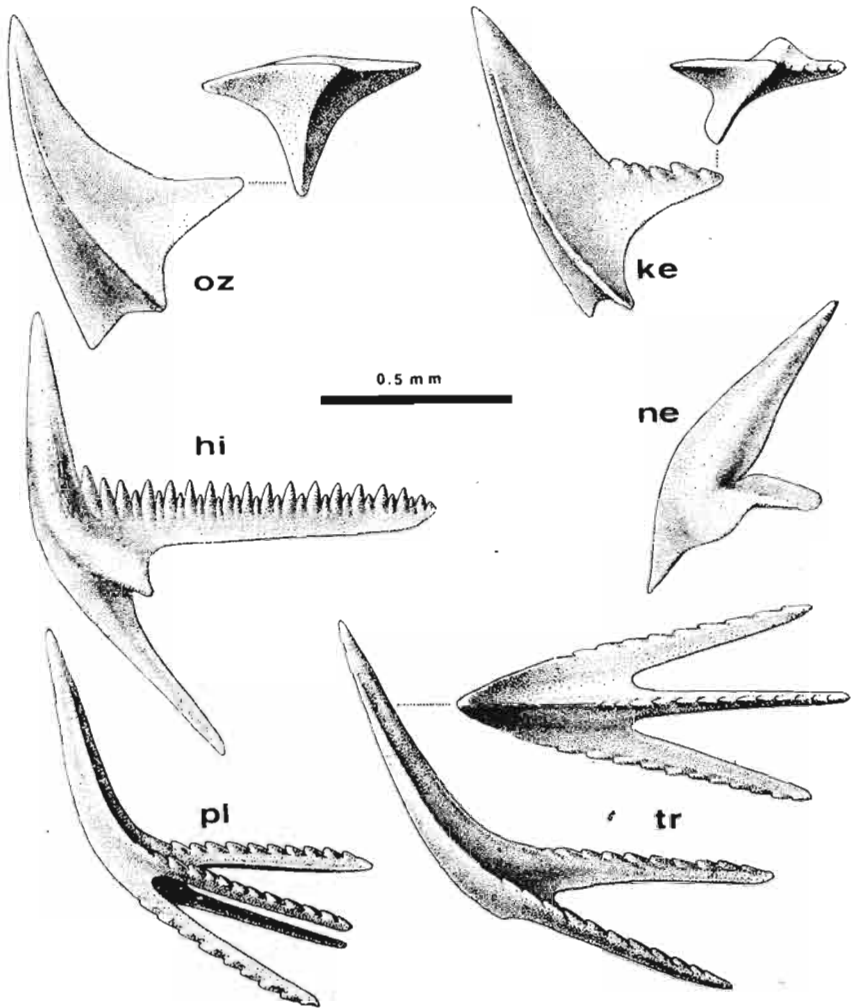robust form of most elements.

Fig. 2. *Baltoniodus bohemicus* sp. n., Klabava Formation, uppermost *Oepikodus evae*
Zone (Arenigian), Svatoštěpánský rýbnik near Mýto, Bohemia. Reconstruction of
particular types of elements of the apparatus.

Description. — *Sp* + *oz* element (pl. 4: 1): to these types of elements I assign robust, undenticulated elements with strongly projecting lateral costae. These elements resemble in outline the *oz* (sagittodontan) element of *Icriodella*, with a weakly developed cusp and deep basal cavity. Variability in shape is small — I have not observed elements with a wide angle between the anterior and posterior processes (amorphognathiform) or any with incipient denticulation.

Tr element (pl. 5: 1): Most specimens are weakly denticulated and have a rather simple shape. These elements display the same type of variability in the sample as the *pl* elements.

Pl element (pl. 5: 2): All processes (in contrast with *B. crassulus*) denticulated: strongly varying in both the degree of development of denticulation and angle of divergence of processes. Some specimens are identical in outline with corresponding elements of evolutionarily advanced species of *Baltoniodus*.

Ke element (pl. 4: 2): Similar to *oz* element of other species, but relatively compressed laterally; posterior process with few, but distinct denticles. Variability small; expressed in development and number of denticles, as well as in elongation of the cusp. It is likely that elements assigned here to the keislognathiform type actually represent the *oz* type.

Hi element (pl. 4: 3, 4; pl. 2: 5): These are relatively robust elements, with a short undenticulated anterior (lower) process, a sharply tipped lateral process and a high, denticulated posterior process. Lateral process with a rounded surface, not homologous with the lateral process of *ke* element, which occurs on the outer side of the element. The shape and distribution of denticles are highly variable, from widely spaced and robust (pl. 2: 5), through irregular (pl. 4: 4) to alternate (pl. 4: 3). The length of anterior process is not significantly variable; in all well-preserved specimens it is relatively short and undenticulated.

Ne. element (pl. 5: 3, 4): Almost identical with a homologous element of *A. deltatus*; that is, it has a short anterior process and a relatively robust cusp. Posterior process considerably shorter than cusp (in contrast to *B. crassulus*). Variability small.

Remarks. — Determination of the relationship between *Baltoniodus bohemicus* sp. n. and *B. triangularis* (Lindström) is of particular importance taxonomically and biostratigraphically. According to Lindström (1971: 31, 35), "*Baltoniodus triangularis* (Lindström, 1955) occurs only in a thin interval at the base of BIIα. It is a clumsy looking species with a wide basal sheath and variable, not seldom sporadic denticulation. Within BIIα, it is succeeded by *B. navis* (Lindström, 1955) which has a persistent and obvious denticulation (...) The oistodiform element (of *B. triangularis*) carries inconspicuous denticles anteriorly." *B. triangularis* was listed as a synonym of *B. navis* by Van Wamel (1974) although he confirmed the fact that early form elements of *B. navis* have weak denticulation and that a continuous transition from *A. deltatus* to *B. navis* took place in his sections. Later forms of *A. deltatus* display an undulation of cristae. Above them (after a short interval occupied by *B. crassulus*) a gradual development of denticulation within the range of *B. navis* occurs. The earliest *sp* elements of *B. navis* illustrated by Van Wamel come from a relatively high horizon, that is, from the *Microzarkodina flabellum* assemblage Zone (section 6, sample 30, pl. 8: 10). The same sample contains ramiform *ke* elements (Van Wamel 1974: pl. 8: 14) with a lateral costa and a denticulated anterior process, *ne* elements with a long anterior process and *oz* elements with widely spaced incipient denticles. Van Wamel (1974, pl. 8: 13) also illustrated *hi* elements that lack denticles on the anterior process, and *pl* elements, with widely spaced incipient denticles, which occur in the *P. navis/P. crassulus* zone (section 6, sample 19). Few *B. navis* elements have been recorded by Van Wamel (1974) as cooccurring with *B. crassulus* in this sample. I doubt whether it is possible to separate elements

objectively (in particular the non-*ne* ones) of such closely related species within
one sample. *B. bohemicus* sp. n. may be identical with these earliest populations
of *B. navis sensu* Van Wamel. The possibility of including these populations in
B. triangularis is another problem.

With regard to *Baltoniodus navis* and *B. triangularis*, Löfgren (1978) found that
"the taxonomic rank of these two taxa is not unequivocal, but there is undoubtedly
a difference between *Prioniodus* (*Baltoniodus*) elements from different levels within
the Early and Middle Volkhovian. The obvious differences between 'early' and 'late'
representatives is stratigraphically important, and these representatives should be
separated at least at subspecies level." All of Löfgren's (1978: 120) statistically
meaningful samples that contain *B. triangularis* elements, also include specimens of
B. navis, but *B. triangularis* is subordinate in those samples. This suggests that
elements referred to *B. triangularis* by Löfgren (1978) are weakly denticulated
morphotypes of *B. navis* and do not represent a distinct temporal species or sub-
species in the *B. navis* evolutionary lineage.

The stratigraphic position of the holotype of *Baltoniodus triangularis* is of key
importance in understanding the relationship between *Baltoniodus triangularis* and
B. navis. The holotype comes from samples at the Bjällum locality in Västergotland,
Sweden (Lindström 1955: pl. 5: 45). The same sample also contains typical elements
of the evolutionarily advanced *B. navis*: a *hi* element with a denticulated anterior
process (*Prioniodina densa*, op. cit.: pl. 5: 20) and a *sp* element with strongly developed
denticulation (op. cit.: pl. 5: 34). These elements were included by Lindström (1971)
in the synonymy of *P. triangularis*, together with *Oistodus linguatus extenuatus*
(Lindström 1955: pl. 3: 42) from sample at Bjällum, which is a typical *ne* element
of *P. navis*. Thus, *B. triangularis* appears so similar to *B. navis* that it may be
considered a subjective synonym of *B. navis* (perhaps its earliest temporal sub-
species). The name *B. triangularis* cannot be used to designate populations that
preceded in time the appearance of well denticulated and showing wide angle of
divergence of processes of *sp* and *oz* elements. *B. bohemicus* may represent this
grade of the evolution of *B. navis* lineage. Then, *B. bohemicus* sp. n. would be a
temporal species (or subspecies) covering the segment of phyletic evolution between
Acodus deltatus and *B. navis*, beginning with the appearance of denticles on
branched elements of the apparatus and extending to the level at which denticles
appear on *ne* elements and distinction between *sp* and *oz* elements developes.

Distribution. — Klabavian of Bohemia, Svatoštěpánský rýbnik near Mýto;
possibly uppermost Billingen of Baltic region.

Baltoniodus sp.

Remarks. — Single *sp* element, robust but with a distinct denticulation; *oz* and
pl elements with indistinctly denticulated processes and a very slender outline, as
well as an *ne* element from Osek belong to some species of *Baltoniodus*. Oz and *pl*
elements of this type occur subordinately even in evolutionarily advanced po-
pulations of *Baltoniodus*. This material is insufficient for a more accurate identifica-
tion of the species. The specimens discussed differ from the elements of *B. bohemicus*
sp. n. from the Klabava Formation in smaller dimensions and dark coloration (the
rock from which they were separated was black). Denticulation of the *sp* element
proves that it represents species considerably more advanced evolutionarily than
B. bohemicus.

Distribution. — Sarkan of Bohemia, Osek (siliceous concretions of the *Corymbo-
graptus retroflexus* Zone).

PALEOECOLOGY OF THE CONODONT ASSEMBLAGE FROM MÝTO

The assemblage of conodonts from a tuffite bed of the Klabava Formation at Svatoštěpánský rýbnik near Mýto contains specimens representing four conodont species, *Scalpellodus laevis* Dzik, *Drepanodus arcuatus* Pander, *Drepanoistodus forceps* (Lindström) and *Baltoniodus bohemicus* sp. n., whose elements make up 72 per cent of all specimens in the sample. *Drepanoistodus forceps* (Lindström) supplied about 18 per cent of the elements. The remaining two species, *Scalpellodus laevis* Dzik and *Drepanodus arcuatus* Pander contributed 5 and 6 per cent respectively of all elements produced by the community of conodonts. If the
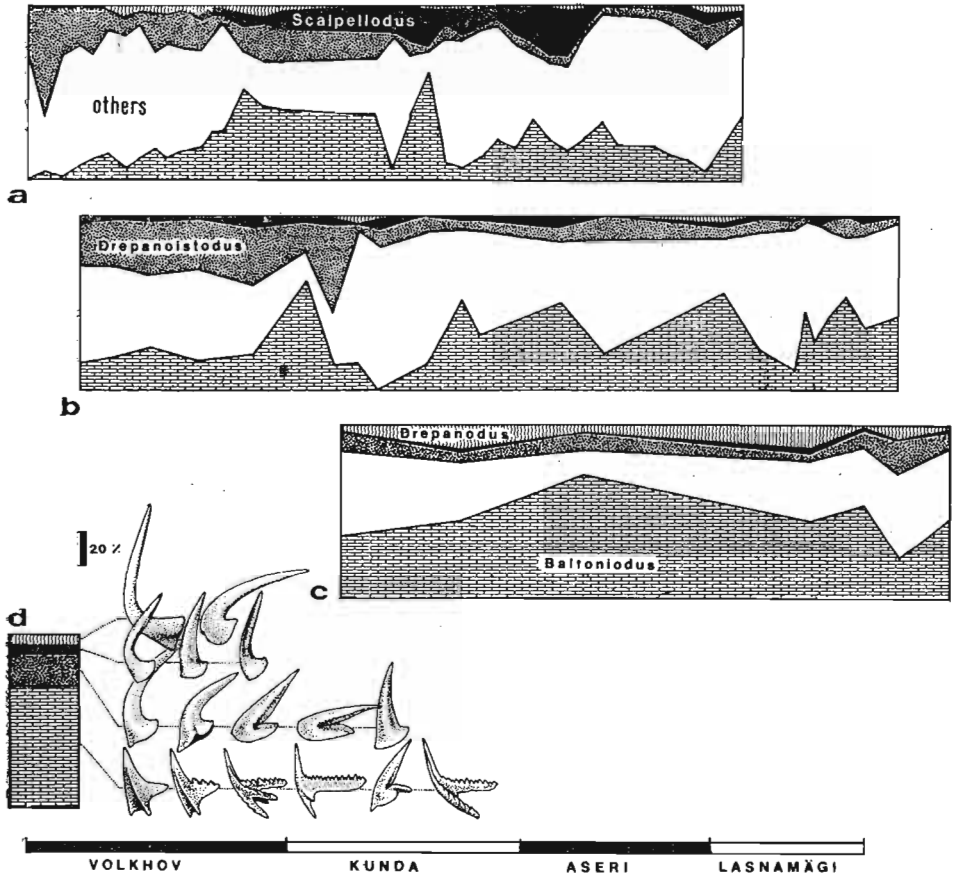
Fig. 3. Composition of the conodont assemblage from Mýto (d) compared with time changes in the composition of the Early Ordovician conodont assemblages from the Baltic biogeographic province. a Jamtland, based on Löfgren's (1978) data, considered sample sizes from 221 to 915 specimens. b Estonia and erratic boulders from northern Poland (source area — southern Sweden and floor of the Baltic sea), data after Dzik (1976), sample sizes 71 to 1898 specimens. c Mójcza Limestone, Holy Cross Mts., Central Poland, data after Dzik (1978), sample sizes 58 to 882 specimens. Note that the distribution of specimens in particular samples is a direct function of relative biological productivity of particular species, not their biomass (Dzik 1979).

number of elements in the apparatus of various species was approximately
the same, as indicated by composition of natural assemblages, the role of
conodonts in the fossil assemblage (disregarding taphonomic factors) was
a function of the role of particular species in biological productivity of
the community. Elements of *Scalpellodus* are somewhat smaller in average
dimensions than elements of *Baltoniodus* and *Drepanoistodus*, whereas
Drepanodus produced much larger elements. If element dimensions were
correlated with body size this might mean that the role of *Drepanodus* in
biomass production was considerably greater than that of *Scalpellodus*.

Species from the Klabavian of Bohemia, or forms closely related to
them, are common in the Lower Ordovician of the Baltic Region and
quantitative proportions in Baltic samples containing them are similar.
That is, species of *Drepanodus* and *Scalpellodus* is greater and species
of *Baltoniodus* are commonly predominant (fig. 3). Unfortunately, I have
no data on the structure of assemblages from the highest Billingen
substage, which in all likelihood are of the same age as the Mýto fauna.
Sample Ot-10 containing *Baltoniodus crassulus* (Lindström) *sensu* Van
Wamel (top of Ottenby cliff, Southern Öland, Sweden; early *Oepikodus
evae* Zone, Upper Billingen) is quite different from the Mýto sample and
is dominated by *Oistodus, Oepikodus, Drepanodus, Paroistodus* and *Scolo-
podus*. Samples from the Volkhovian and Kundan (cf. Dzik 1976, 1978;
Löfgren 1978) are more distinctly similar. All samples known to me from
the Baltic Region and the Holy Cross Mts. differ conspicuously, however,
in containing twice as many species as are found at Mýto. These dif-
ferences are clearly visible on diagrams illustrating the percentage of
particular species and changes in faunal composition that took place in
time (fig. 3). Application of a diversity index, calculated according to the
same principles as the Shannon information index, for the purposes of
comparing fossil assemblages, was suggested by Berry *et al.* (1979). The
diversity index calculated according to the Shannon's equation for the
conodont assemblage of Mýto is D = 0.40 and departs conspicuously from
that calculated for most Baltic samples, such as those of Jämtland
(Northern Sweden; Löfgren 1978) which are closest in age and display
the following values: sample J. 74—28, D = 0.76 (n = 323) and sample
J. 69—70, D = 0.76 (n = 489), sample from the Upper Volkhovian of
Sukhrumägi, Estonia (Dzik 1976); D = 0.67 (n = 546), from *O. evae* Zone
of Ottenby, Öland, D = 0.85 (n = 1965), erratic boulders of the *P. originalis*
Zone (Dzik 1976): sample E-116, D = 0.73 (n = 1898), sample E-119,
D = 0.75 (n = 217). A similar value for the diversity index is displayed
by a sample, closest in age, from the Mójcza Limestone (Holy Cross Mts.,
Poland, Dzik 1978): MA-14, D = 0.74 (n = 725). One may find in the
Baltic sections particular samples displaying rather small diversity, for
example, sample J. 70—8 (Löfgren 1978) in which D = 0.65 (n = 706), but
that sample is not similar in composition to the one from Mýto and

contains representatives of ten conodont species. The low value of the latter index results from the fact that the sample is dominated by two species, *Baltoniodus praevariabilis medius* (Dzik) and *Microzarkodina ozarkodella* Lindström.

It seems unlikely that the structure of the assemblage from Mýto could correspond to a random fluctuation in the structure of the Lower Ordovician conodont faunas of Bohemia. Thus, the data presented above may be considered to support the thesis of a cold-water character of the Lower Ordovician basin of Bohemia (Spjeldnaes 1967; Havliček and Branisa 1980). This is indicated both by the diversity-index value and by the small absolute number of species represented in the sample. In the Klabava sample, there occur exclusively the species known also from the Baltic Region, which is considered to have been in the cold-climate zone (Lindström 1976). At the same time, these are species that dominate quantitatively in Baltic assemblages. On the other hand, no species common to the Baltic basin and the American equatorial seas, for example, representatives of Ozarkodinina and Oistodontidae, occur in Bohemia.
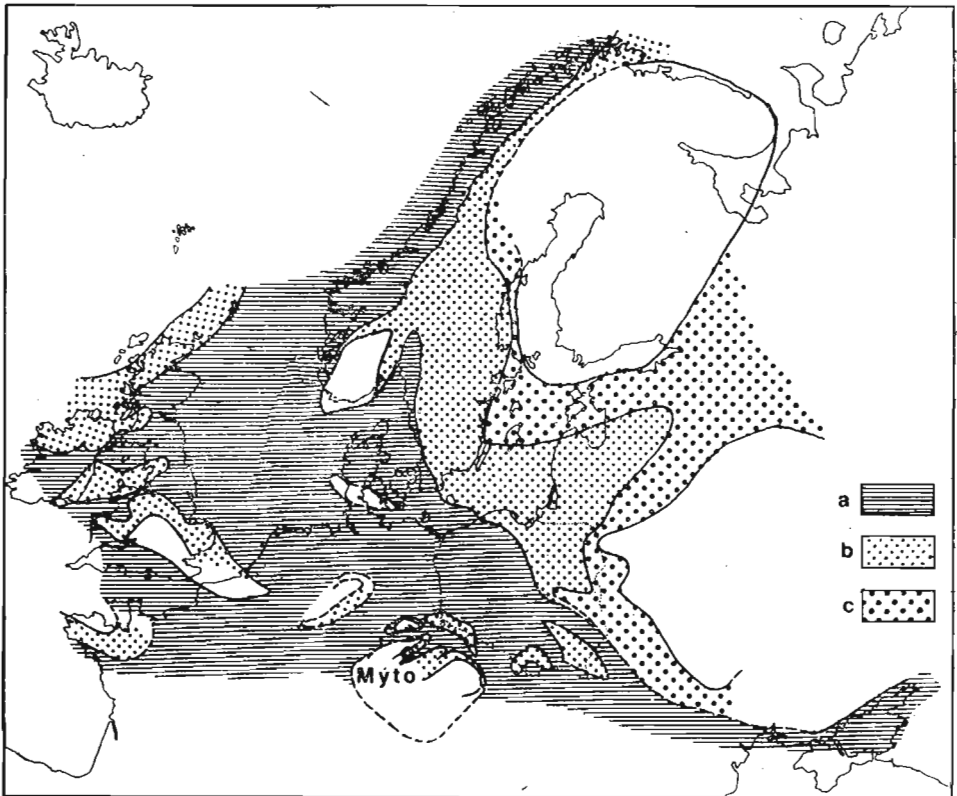

Fig. 4. Facies distribution in the Early Ordovician of Europe. Not palinspastic; after Dzik (1978); *a* graptolite shales and flysch; *b*, *c* deep and shallow sublittoral facies (mainly carbonates).

EVOLUTIONARY AND PALEOBIOGEOGRAPHICAL RELATIONSHIPS
OF THE CONODONTS FROM THE KLABAVA FORMATION

Late Latorpian conodont faunas are know from numerous sections
(i.a. Bergström and Cooper 1973; Landing 1976; Löfgren 1978; Fåhraeus
and Nowlan 1978; Tipnis *et al.* 1978; Cooper 1981) in many different
parts of the world. To determine the age interval of the Mýto fauna
sections that include parts of the *Acodus → Prioniodus* and *Acodus →
→ Baltoniodus* transitions and whose descriptions are based on recon-
structions of conodont apparatuses are particularly important. These are
primarily sections of the Emanuel Formation, Australia (McTavish 1973),
the San Juan Formation, Argentina (Serpargli 1974) and the Bruddesta
Formation, Sweden (Van Wamel 1974).

Outside the Baltic Region, faunas of about the same age as those
of Mýto are very little known in Europe. In the Holy Cross Mts., the
area closest geographically and faunally to the Baltic Region, a fauna
of this type occurs in calcareous intercalations within the Bukówka
Sandstone (Bednarczyk and Biernat 1978) but, unfortunately, it has not
yet been described in detail. A list of species presented by Bednarczyk
(op. cit.: table 2) includes forms that should not occur together, for
example, *Paroistodus amoenus, P. parallelus* and *Baltoniodus navis.* The
fauna of Rzeszówek in the Kaczawskie Mts (part of the Sudeten Moun-
tains) probably younger than Klabavian (Baranowski and Urbanek 1973),
has also not been described as yet in terms of conodont-apparatus taxo-
nomy. In Central Europe, this is the only non-Late Ordovician fauna
that displays distinct relationships with the North American Midcontinent
fauna (Lindström 1976).

The only Central European faunas described that may by closely
related to those of Bohemia come from the Frankenwald (Sannemann
1955). Insofar as these faunas can be "translated" into apparatus taxo-
nomy, they contain:
Fundpunkt 1, 1 km NW Baiergrün (Randschieferserie) — *Cornuodus
longibasis* (Lindström, 1955), *Protopanderodus* cf. *rectus* Lindström,
Drepanoistodus cf. *forceps* (Lindström), *Acodus?* sp.
Fundpunkt 2, Hoher Berg, NNO Baiergrün (Randschieferseries) — *Bal-
toniodus* sp. (*praevariabilis* Fåhraeus), *Drepanoistodus* sp., *Dapsilodus* cf.
viruensis (Fahraeus).
Fundpunkt 3, between Thron and Schönwald — *Drepanodus franconicus*
(Sannemann), *Drepanoistodus* cf. *forceps* (Lindström).

The fauna of Fundpunkt 2 is probably considerably younger than that
to Mýto, and the fauna of Fundpunkt 1 may be of the same age or
somewhat older. The fauna of Fundpunkt 3 was assigned by Lindström
(1976) to a separate conodont zoogeographical province known as the
'*franconicus* fauna'. According to Lindström, that fauna also occurs in

the Lower Loire Valley, France, where it is associated with elements of the North' American *quadraplicatus* fauna. *Drepanodus franconicus*, which differs from the Baltic *D. arcuatus* in having more arcuately curved cusp, is a characteristic element of this fauna. Except for this species, all others described by Sannemann (1955) may be identical with ones known from the Baltic Region. According to Lindström's (1976) interpretation, the fauna of Fundpunkt 3 is older than that of Mýto.

In the Massif Armoricain, France, another region related paleobiogeographically with Bohemia, conodonts are known only from the Llandeillan Postolonnec Formation, which is considerably younger than the Klabavian and Sarkan. That fauna is decidedly different than contemporaneous Baltic ones (Lindström *et al.* 1974).

As mentioned above, *Baltoniodus bohemicus* sp. n. can be compared, in the degree of development of its denticulation and the structure of apparatus, with *Prioniodus transitans* McTavish from the Emanuel Formation of Canning Basin, Australia, *Baltoniodus pseudoramis* (Serpagli) from the San Juan Formation, Argentina, as well as with *Baltoniodus crassulus* (Lindström) *sensu* Van Wamel, 1974 (= *Gothodus costulatus sensu* Lindström, 1971) and *B. triangularis sensu* Lindström, 1971 from earliest Volkhovian of Sweden. Determinig the actual relationships of *B. bohemicus* sp. n. implies, from the biostratigraphic viewpoint, the necessity of determining whether the Mýto fauna is older or younger than the *P. elegans* Zone.

I prefer to interpret Bohemian species as a form close to the oldest *Baltoniodus* and not to *Prioniodus* for the following reasons:
(1) In the *A. deltatus* → *P. transitans* → *P. communis* lineage (cf. McTavish 1973), the *sp* + *oz* element displays an early appearance of denticulation on its posterior process, whereas the comparable element of early species of *Baltoniodus* and *B. bohemicus* is undenticulated. Ramiform elements of *P. transitans* are also considerably more delicate than those of *B. bohemicus*.
(2) Conodonts associated with *B. bohemicus* sp. n., although not biostratigraphically diagnostic, suggest post-*P. elegans* Zone time. A similar age is suggested (although it is a rather risky interpretation) by structure of the assemblage, which resembles that of Early Volkhovian assemblages rather than Late Hunnebergian or Early Billingenian ones.
(3) The absence of unequivocally non-Baltic species in the Mýto assemblage suggests that the Bohemian conodont fauna have a closer biogeographic relation with those of the Baltic Region than with Australian or Argentinian ones.

The relationship between *Baltoniodus bohemicus* sp. n. and other known species of *Baltoniodus* cannot be unequivocally determined on the basis of available data. The relationship between *B. crassulus* and *B. bohemicus* seems to be of particular significance because the two
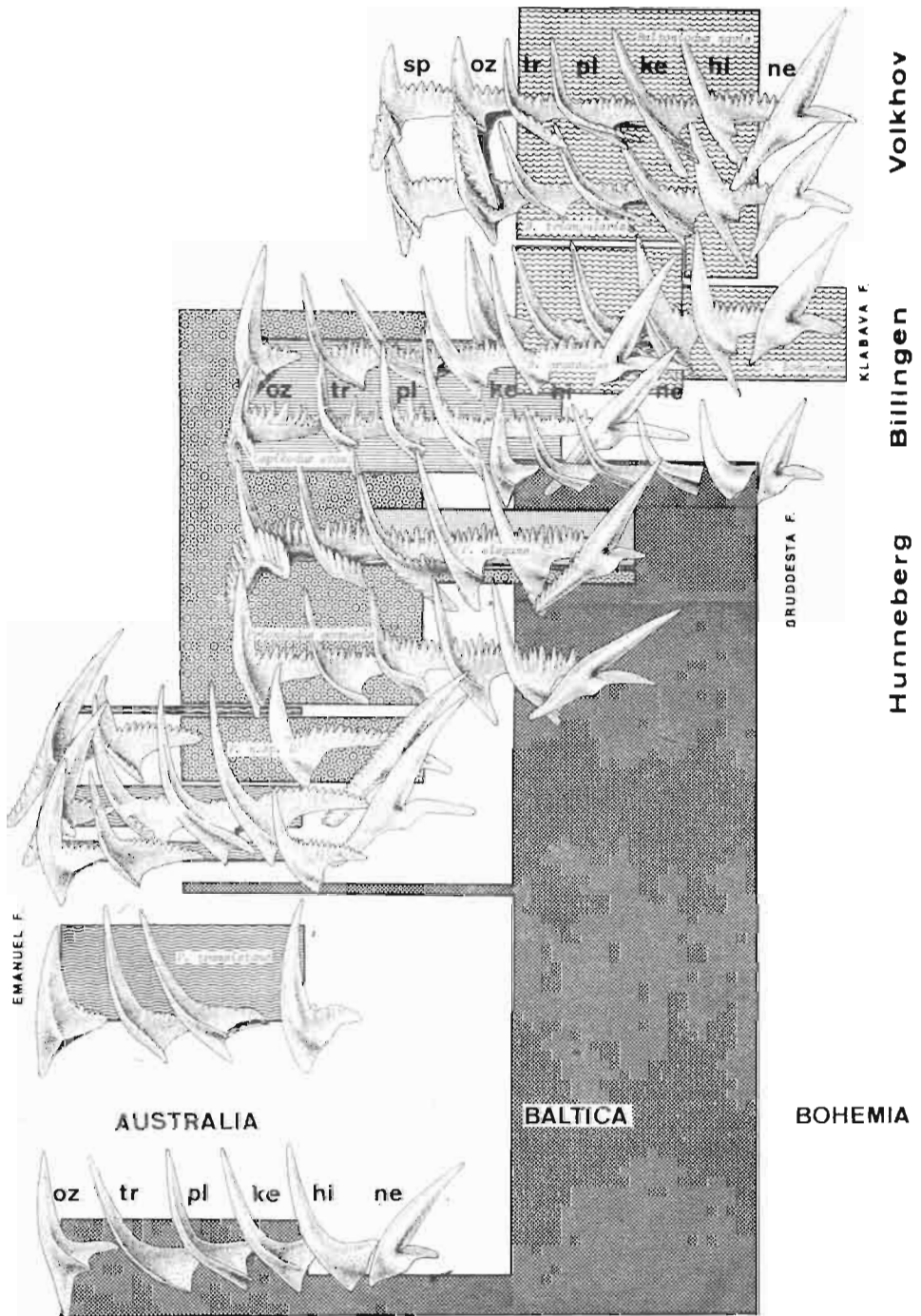
Fig. 5. Proposed interpretation of evolutionary and paleozoogeographic relationships of *Baltoniodus bohemicus* sp. n. Data partially after McTavish (1973) and Van Wamel (1974).

species differ from one another generally only in the shape of the posterior process of their *ne* elements. There are at least two possible types of relationships between them, however, which require testing:

(1) *B. crassulus* and *B. bohemicus* sp. n. are parts of the same phyletic sequence and represent two temporally distinct segments of one species evolving in its entire area of distribution. In this case, one would need to determine the place of *B. bohemicus* sp n. in this evolutionary sequence and demonstrate that it was an ancestor or descendant of *B. crassulus*. If it is profitable to speculate in this direction, one would prefer a second solution. That is, due to the robust form of *B. bohemicus* elements, its transitional place between *B. crassulus* and *B. triangularis sensu* Lindström, 1971, seems to be more probable. The form of the *ne* element of the latter, which departs from the postulated evolutionary trend from *A. deltatus* → *B. bohemicus* → *B. triangularis*, as well as the presumable distinct zoogeographic dissimilarity of the Bohemian ecosystem (discussed below), seem to be arguments against a close relationship between *B. bohemicus* and *B. crassulus*.

(2) *B. crassulus* and *B. bohemicus* sp. n. are species that evolved allopatrically from *A. deltatus* and are at least partially coeval (fig. 5). This interpretation does not preclude a relationship between *B. bohemicus* and *B. triangularis*. *B. navis* early form *sensu* Van Wamel, 1974, could represent a late population of *B. bohemicus* whose range was extended to include the Baltic province.

Hypothesis 1 is difficult to falsify, because such falsification would require unequivocal proof of discontinuity ni the temporal succession from *B. crassulus* → *B. triangularis* (which may be impossible within the methodological limits of paleontology), or of geographic discontinuity between the Baltic and Bohemian populations of *Baltoniodus* (which is impossible to attain in practice). Hypothesis 2 may easily be falsified by proving the continuity of the *B. crassulus* → *B. triangularis* transformation. For this reason, I assume it in the present paper (fig. 5).

SIGNIFICANCE OF NON-CONODONT FAUNAS FOR A BIOSTRATIGRAPHIC CORRELATION AND BIOGEOGRAPHICAL ANALYSIS OF THE BOHEMIAN EARLY ORDOVICIAN

The data presented above indicate a close relationship or identity of the Lower Ordovician conodont faunas of the Barrandian and the Baltic Region and oppose previously accepted views concerning biogeographic dissimilarity of the two regions. Because the biostratigraphic and paleozoogeographic consequences of accepting this interpretation of Klabavian and Sarkan conodont faunas are far reaching, it seems necessary to confront them with data concerning other faunal groups and

possibly determining the causes of such a great differentiation of some and identity of some other faunas occurring in these regions. Equally significant is the necessity of checking the biostratigraphic conclusions that result from analysis of relationships of conodont fauna by means of data from a similar analysis of other taxonomic groups.

Fossil assemblages from clastic deposits of the Klabava Formation are of low diversity (cf. Havliček and Vaněk 1966). Only graptolites and trilobites have been described in detail taxonomically. Graptolites have been the basis for age correlation between the Bohemian Ordovician and that of other regions. Beds that crop out of the Svatoštěpánský rýbnik locality were included by Bouček (1973) and Kraft (1977) in the local *Tetragraptus reclinatus abbreviatus* Zone. On the basis of a general character of fauna, Bouček (1973) correlates the *T. r. abbreviatus* Zone with the *Isograptus gibberulus*[1] subzone of the *D. extensus* Zone of the British standard. This dating is similar to the one that results from the above-presented interpretation of evolutionary relationships of conodonts. According to this interpretation, the Mýto beds could correspond to the uppermost part of the *P. evae* Zone; or, in conformity with the correlation of graptolite and conodont zones (Bergström and Cooper 1973), to the boundary between the *D. nitidus* and *I. gibberulus* subzones. The degree of paleobiogeographic diversity of graptolite faunas of the Bohemian and Baltic Lower Ordovician is difficult to determine on the basis of available data. However, it is possible to state that many common Bohemian forms are unknown in the Baltic Region (cf. Bouček 1973; Berry 1979). Analyzing graptolite assemblages from the biostratigraphic and paleozoogeographic viewpoints, one should bear in mind their peculiar biological character, namely the presumably hermaphroditism or parthenogenesis of graptoloid graptolites (Kozłowski 1960; Spjeldnaes 1963). It follows from the manner of colony formation in graptolite (Rickards and Crowther 1977; Andres 1980) that evolution of rhabdosome form is evolution in behavior and not in animal morphology as is the case with other colonial organisms. Thus, neither the population concept of species, nor the methodology of biostratigraphic conclusions based on it, are applicable to the Graptoloidea (Dzik and Trammer 1980). For example, the problem of British and American correlations of the *D. bifidus* Zone (Bergström and Cooper 1973; Fåhraeus 1977), is a symptom of problems resulting from the equivocality of graptolitic biostratigraphy. From this viewpoint, it would be also necessary to consider the significance of the diachronous appearance of biserial diplograptids in the Baltic Region and Bohemia (Bulman 1963; Jenkins 1980).

Dissimilarity of the trilobite faunas of the Baltic Region and Bohemia (Whittington and Hughes 1972, 1973) has been strongly emphasized. This dissimilarity is more distinctly visible in Sarkan than in the Klabavian, due mostly to differentiation of the asaphids in the Baltic fauna. However,

it is not clear to what extent this is the result of paleozoogeographic dissimilarity of entire regions or to what extent the differences ensue from a dissimilarity of the facies, carbonate ones in the Baltic Region and clayey ones in Bohemia, from which most paleontological materials come. This also applies to Bohemian relationships of trilobites from the Arenigian of Thuringia (Volk 1960; Struve 1971). Convergence of Baltic and Bohemian assemblages in the Upper Ordovician (a.o. Kielan 1959) is related to a convergence in facies. The present remarks may be also applied to brachiopods (cf. Williams 1973; Sheehan 1973; Havliček and Branisa 1950).

The single species of gastropods mentioned by Havliček and Vaněk (1966) from the Klabava Formation, that is, the hyperstrophic *Mimospira helmhackeri* (Perner), is unimportant to paleozoogeographic considerations, although its close relative may be found in the Baltic Ordovician (Wangberg-Eriksson 1979; Dzik 1983). A relatively diverse fauna of monoplacophorans and gastropods from Šarka Formation concretions, however, requires detailed comparison with Baltic forms. According to the assumption adopted a priori on the dissimilarity of Baltic and Bohemian faunas, the possibility of their relationships is not even discussed in monographs (Horný 1963; Yochelson 1963) concerning gastropods and monoplacophorans of Bohemia and the Baltic Region. At least some of the species described from the Barrandian, for example, the bellerophontid monoplacophoran *Sinuitopsis neglecta* Perner, also occur in the Baltic region (Dzik 1981).

The typically "Mediterranean" pelecypod *Babinka* also occurs in the Kundan of the Baltic Region (Soot-Ryen 1969). The ribeirids, a Mediterranean group of mollusks related to pelecypods, are not uncommon in the Baltic region, although they have not yet been described.

Opercula of Baltic hyoliths are not known well enough to allow a comparison between them and hyoliths of the Šarka Formation (Marek 1976), but relationships within the limits of particular lineages and migrations between these provinces are probable (Dzik 1978b, 1980).

Echinoderms are a group of organisms that most distinctly express dissimilarity between the Baltic and Bohemian ecosystems. However, comparisons are possible only beginning with the Sarkan because echinoderms are unknown in both the Bohemian Klabavian and the Baltic Latorpian. There is almost no similarity between the echinoderm fauna of the Šarka Formation and that of the Baltic Lower Ordovician. Particularly spectacular is the abundance of carpoids in the Bohemian Lower Ordovician and their complete absence from the Baltic region. Only in the Lower Caradocian (Kukrusean) does the first Baltic carpoid appear. It is *Heckericystis* which is closely related to Lower Ordovician carpoids of Bohemia and probably descended from them.

Some hope for explaining the paleozoogeographic dissimilarity of the

Bohemian and Baltic regions may focus on the ostracods, which are equally as common in the Klabavian as in the Sarkan and have recently been investigated by Dr Miroslav Krůta, Ústředni geologický ústav, Prague. The fairly diverse assemblage of ostracods from Svatoštěpánský rýbnik includes forms that display distinctly Baltic affinities (fig. 6) and this is not an exception among Bohemian Ordovician ostracods (Shallreuter and Krůta 1980). One of these species (fig. 6a) is morphologically transitional between Baltic species of *Glossomorphites* (Hessland 1949) and later species of the Bohemian *Cerninella* (Jaanusson 1957; Přibyl 1966, 1979). Among Baltic ostracods, forms of *Glossomorphites* described by Hessland (1949) from the Lower Ordovician of the Siljan area, Central Sweden are closest to this species. Ten species were separated by Hessland within an interval from Upper Volkhovian to Aserian, but this differentiation seems to include, at least partially, sexual dimorphism and intrapopulational variability. The species from the Klabava Formation differs from its nearest morphotype, *G. tenuilimbatus* (Hessland, 1949), in narrower lobes and a very narrow sulcus (S 3) between its posterior lobes (L 3 — L 4).
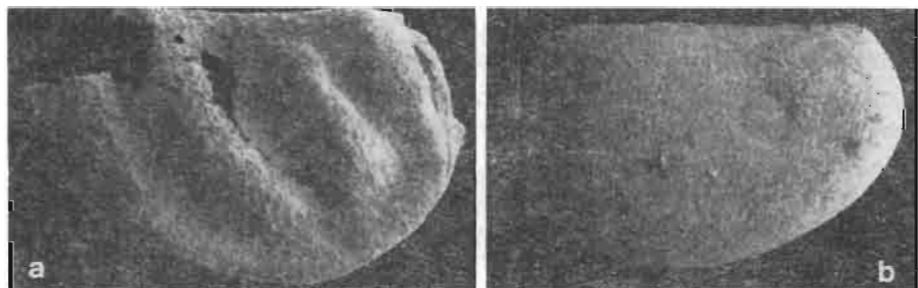

Fig. 6. Ostracods from the Klabava Formation (Svatoštěpánský rýbnik) showing Baltic affinities. a *Cerninella* sp. n. b *Pyxion* sp. Both x 80.

The differences, as compared with the Bohemian species *Cerninella complicata* Přibyl, 1966 from the Šarka Formation (Přibyl 1966, 1979), the closest in age, are of a quite opposite character. *C. complicata* has sharp lobes, a considerably wider S 3 and its histial ridge (possibly homologous with the connecting lobe of *Tallinella*) is situated somewhat above the lower margin of the test. We can presume that the Bohemian species of *Cerninella* are a phyletically evolving assemblage of populations. The trend of evolution is determined by changes in the shape (expansion) of S 3 and the conversion of a histial ridge into a connecting ridge. If we determine the ratio of the width of S 3 to the distance between the dorsal margin of test and the connecting ridge, this index for the species from the Klabava Formation (fig. 6a) amounts to about 3.1; to about 2.1 for *C. complicata* from the Šarka Formation; and to about 1.5 for *C. bohemica* from the Vinice Formation. At the same time, changes within the limits of the Baltic genera *Glossomorphites* and *Sigmo-*

opsis are expressed in the extension of lobes marked by a peculiar ornamentation and in the contraction of sulci.

Divergent evolution of *Cerninella* and the *Glossomorphites-Sigmoopsis* stock may be interpreted as an example of allopatric speciation resulting from a divergent phyletic evolution of geographically isolated populations. It is likely that in the Early Arenigian (Klabavian) a Baltic representative of *Glossomorphites* settled the epicontinental sea of the Moldanubicum and there started an independent evolution, which led in Bohemia to the formation of *Cerninella* convergently likened to the Baltic *Tallinella* (cf. Jaanusson 1957). Of course, the direction of expansion could also have been in the opposite direction, but no data are available concerning earlier faunas of ostracods, either in Bohemia or the Baltic Region.

Nektonic organisms, such as nautiloids, which are not so closely connected with facies as the benthonic ones discussed above and, in contrast to the graptolites, have an unequivocal biological character, may serve for verification of the hypothesis of the divergent evolution of Bohemian and Baltic communities in the Early Ordovician. Unfortunately, no data on nautiloids from the Klabava Formation are available. Five species unquestionably dissimilar to each other have so far been described from the Šarka Formation. They are: *Bathmoceras complexum* Barrande, 1856, *Bactroceras sandbergeri* (Barrande, 1868) (= *Tretoceras parvulum* Barrande, 1868; Dzik 1982a), *Ormoceras bonum* (Barrande, 1868) (? = *Orthoceras occultum* Barrande, 1868), *Endoceras? peregrinum* (Barrande, 1868) and *Intejoceras? novator* (Barrande, 1868). The first four are probably conspecific with Baltic species of the same genera (cf. Holm 1894, 1898; Sweet 1958; Dzik 1984). On the other hand, there are no equivalents of *I.? novator* in the Baltic Region. No nautiloids with such a wide, cylindrical central siphuncle are known in the Baltic Lower Ordovician. The only species with a phragmocone structure of this type that I have observed represents a *Intejoceras* from the Llandeillian of Siberia (Dzik 1984). The lack of data on internal structure of the siphuncle (especially siphuncular deposits) and on the shape of the apical part of shell precludes the possibility of accurately comparing Bohemian and Siberian forms.

Irrespective of the Baltic chronostratigraphic unit to which the nautiloid fauna from the Osek (Sarkan) corresponds, it is quite different in structure than Baltic Early Ordovician fauna. Puzzling is the absence from the Bohemian fauna of the orthoceratids, lituitids and tarphyceratids, which dominate Baltic faunas. On the other hand, Baltic faunas rarely contain *Bathmoceras* or *Bactroceras*. If we take into account the possibilities of migration of nautiloid populations, as well as of a *post-mortem* transportation of their floating shells, these differences may constitute a basis for the opinion that the Baltic and Bohemian Early

Ordovician provinces belonged to two different zoogeographic realms (in the meaning defined above). Characteristically, the Baltic region is marked by a considerably smaller differentiation of tarphyceratids than the North American Midcontinent. This confirms existence of a (climatic ?) gradient: Midcontinent — Baltica — Moldanubicum (fig. 7).

CONCLUSIONS

A distinct paleobiogeographic boundary, separating Early Ordovician realms, the Baltic (or rather North Atlantic, see Sweet and Bergström 1974) one including marine epicontinental ecosystems (provinces) of the East European Platform (Baltica), the region of Oslo, Norway, and the Holy Cross Mts, Poland, and the Bohemian one including epicontinental ecosystems of Moldanubicum, Atlas, Brittany, Montagne Noire, and perhaps the Sudeten Mts and several other massifs, extends between the Holy Cross Mts and the Moldanubicum (and perhaps even the Sudeten Mts). The Moldanubicum ecosystem is marked by dominantly fine-clastic and pyroclastic sedimentary rocks, a small degree of differentiation of nektonic faunas (conodonts and nautiloids) and, presumably, cold-water benthonic assemblages. The Holy Cross Mts ecosystem is characterized by carbonate rocks, with a considerable influx of sandy deposits in the Arenigian. Conodont faunas are marked by a diversity index identical with that of Baltic ecosystem faunas. Also identical or closely related are nautiloid assemblages and, presumably, benthonic assemblages of the temperate climate.

The boundary between the Bohemian (Mediterranean) and the North Atlantic realms was selectively penetrable by various ecological and taxonomic groups of organisms. Only a few Early Ordovician groups of organisms did not cross this boundary. Here belong primarily the Carpoidea (Echinodermata), which, although abundant in the Šarka Formation, are unknown from the Baltic Early Ordovician, and the bryozoans, which are an important component of the Volkhovian, Kundan and Lasnamägian assemblages (also of pelagic red *Orthoceras* limestones) in the Baltic region and the Holy Cross Mts but are thus far unknown from the Early Ordovician of Bohemia. With regard to the majority of the remaining groups of benthonic organisms, some single species succeeded now and then in penetrating the boundary between the provinces and, after taking possession of an appropriate niche, developed in the other ecosystem a new evolutionary lineage independent of the initial

Fig. 7. Early Ordovician palaeogeography of the regions discussed. Equal-area projection; position of the main land masses after Ziegler *et al.* (1979), Scotese *et al.* (1979), and Bergström (1979). Facies distribution after Ross (1976), Havliček (1976), McTavish and Legg (1976), Dzik (1978), and others. Arrows indicate supposed directions of oceanic currents.
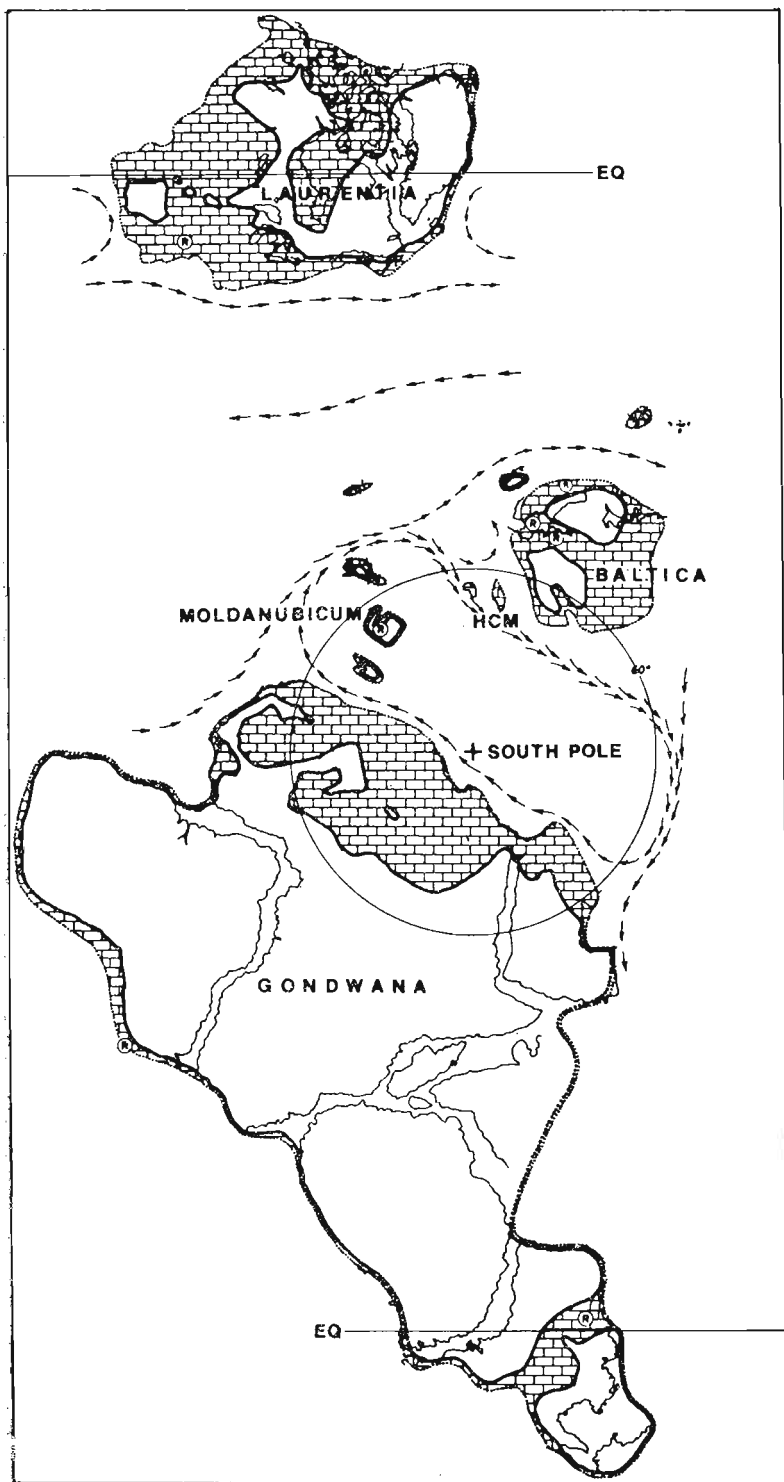
one. This concerns the ostracods, bellerophontid and hyolithid monopla-
cophorans, bivalves and, probably trilobites. However, this boundary was,
characteristically, an efficient barrier to a considerable part of the nec-
tonic nautiloids and planktonic graptolites. Conodonts seem to be the
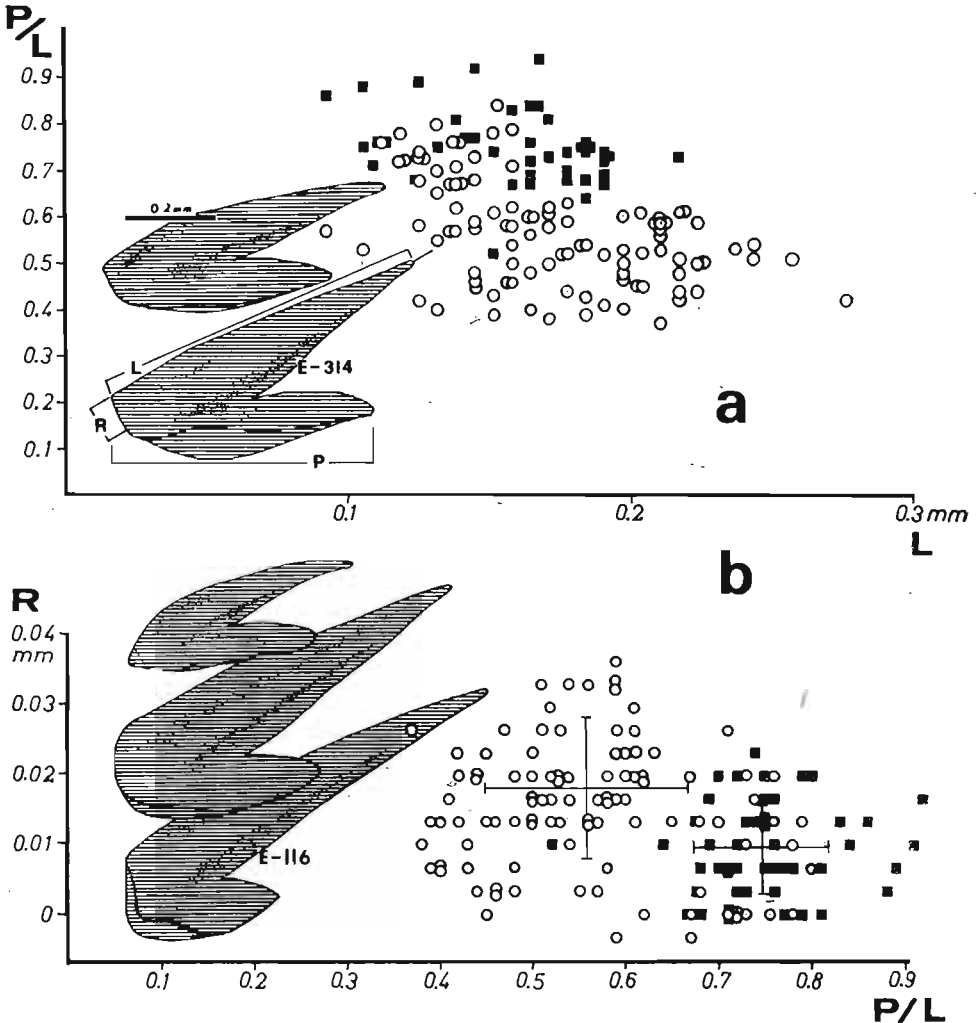only group to which this boundary was not an obstacle to migration,

Fig. 8. Variability of *ne* elements in Baltic populations of *Drepanoistodus forceps*
Lindström, 1955 from the *O. evae* Zone (black sqares, sample A from the erratic
boulder E-314) and from the *P. originalis* Zone (circles, sample E-116). Added contours
of the extreme morphotypes occurring in the samples. a. Index of elongation of the
posterior process plotted against length of the cusp. b. Index of elevation of the
anterobasal corner plotted against the index of elevation of the posterior process;
standard deviations for both indexes indicated. Note that ranges of standard
deviations of the elongation index do not overlap, separation of these samples into
two distinct temporal subspecies is thus substantiated although large samples with
well preserved specimens are necessary to identify these subspecies.

although, as compared with that of the North Atlantic realm, the assem-blage of conodonts from the Klabava Formation is impoverished.

Paleogeographic reconstruction do not reveal the existence of geo-graphical barriers (for example, continents) between Bohemia and the Holy Cross Mts (fig. 7; the Holy Cross Mts, Sudeten Mts and Moldanu-bicum are interpreted as parts of successive island arcs, connected first with Baltica and, after the Caledonian orogeny, with Laurasia; their final consolidation and integration with Laurasia took place in the Hercynian orogeny). Due to the postulated situation of Gondwana and Baltica, the geographic distances between the Moldanubicum and Holy Cross Mts plates could not have been great enough to enable an explanation of such great faunal differences by a simple climatic gradient. On the basis of a knowledge of the distribution of continents, however, one can conjec-ture the marine current system and the climatic boundaries determined by their convergence (van Andel 1979; Schopf 1980). I suggest assuming that the zone of subpolar ("Antarctic") convergence occured between the two plates. With such an assumption, the ecosystems belonging to the Bohemian (or Mediterranean) realm (Moldanubicum, Massif Armoricain, Massif Central, Atlas) will be included within the limits of convergence in the cold zone (fig. 7). The temperate-water ecosystems of Baltica, Oslo, and the Holy Cross Mts will be situated just north of the conver-gence. Changes in the situation of the convergence in relation to islands arcs associated with continental plates undoubtedly constituted an im-portant factor in facilitating expansion of sublittoral and littoral faunas independently of the continental drift. The insensitivity of some groups of organisms (for example, conodonts) to convergence may result from their belonging to the psychrosphere (cf. Seddon and Sweet 1971; Berg-ström and Carnes 1977; Klapper and Barrick 1978). Also noteworthy is the fact that marine currents system resulting from the assumed distribu-tion of continents (fig. 7) explains the relationships between the Baltic conodont faunas and the Australian tropical faunas and, at the same time, their dissimilarity to the faunas of the North American Midcon-tinent, which were situated in the same climatic zone as Australia.

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JERZY DZIK

DOLNOORDOWICKIE KONODONTY BARRANDIENU A CZESKO-BAŁTYCKIE POKREWIEŃSTWA FAUNISTYCZNE

Streszczenie

W formacjach klabawskiej i szareckiej dolnego ordowiku okolic Pragi stwierdzono występowanie konodontów o bałtyckich pokrewieństwach. Szczególnie obfitują w konodonty wapniste tufity górnej części formacji klabawskiej, odsłaniające się w stanowisku Svatotoštěpánský rybník koło Mýta. Zespół konodontów jest tam zdominiowany przez nowy gatunek z rodzaju *Baltoniodus*, przy znacznym udziale znanych z regionu bałtyckiego gatunków rodzajów *Drepanoistodus*, *Scalpellodus* i *Drepanodus*. *Baltoniodus bohemicus* sp. n. jest, pod względem stopnia rozwoju ząbkowania poszczególnych elementów aparatu, pośredni pomiędzy *Acodus deltatus* (bez ząbków) a *B. crassulus* i *B. triangularis sensu* Lindström, 1971 (z zaczątkowym ząbkowaniem większości elementów). Być może obejmuje on, obok populacji czeskiej, również najstarsze szwedzkie populacje *B. navis sensu* Van Wamel, 1974. Zgodnie z tą interpretacją, górna część formacji klabawskiej (i tym samym piętra klabawskiego) odpowiada wiekowo pograniczu bałtyckich pięter latorp i wołchow.

Mimo występowania bliskich lub nawet identycznych z bałtyckimi gatunków, zespół konodontów z formacji klabawskiej zdecydowanie różni się od podobnych zespołów bałtyckich bardzo niskim zróżnicowaniem taksonomicznym oraz odmiennymi proporcjami ilościowego udziału poszczególnych gatunków. Interpretuje się to jako jeszcze jedno potwierdzenie zimnowodnego charakteru morskiego ekosystemu Moldanubiku we wczesnym ordowiku. Stosunkowo ścisłe powiązania konodontów z czeskiego i bałtyckiego ordowiku kontrastują ze znaną od dawna odmiennością faun trylobitów (Whittington and Hughes 1972, 1973), ramienionogów (Williams 1973; Havlíček and Branisa 1980), szkarłupni i bentonicznych mięczaków (Marek 1976). Fauna łodzików z formacji szareckiej, obok gatunków prawdopodobnie wspólnych z regionem bałtyckim, zawiera też formy z ordowiku bałtyckiego nieznane (por. Dzik, 1984), różni się także ilościowym udziałem poszczególnych grup taksonomicznych. Fauny małżoraczków z Czech są znacznie słabiej poznane od równowiekowych, dolnoordowickich faun bałtyckich, dostępne dane wskazują już jednak na ich znacznie mniejsze zróżnicowanie i pogłębiającą się w trakcie wczesnego i środkowego ordowiku odrębność (Přibyl 1979). W nieopisanym dotąd zespole małżoraczków z formacji klabawskiej występują jednak gatunki o wyraźnie bałtyckich pokrewieństwach (fig. 6), są bowiem powody do przypuszczenia, że

bałtycka linia ewolucyjna *Glossomorphites* wywodzi się ze wspólnego pnia z czeską linią *Cerninella*.

Zjawisko wybiórczego przenikania pomiędzy ekosystemami bałtyckim, świętokrzyskim i czeskim niektórych grup organizmów (głównie nektonicznych łodzików i konodontów oraz planktonicznych graptolitów), przy zupełnej niemal separacji wielu grup bentosu, znajduje wyjaśnienie w palinspastycznej rekonstrukcji rozmieszczenia lądów w dolnym ordowiku (fig. 7). Wynika z niej, że pomiędzy kontynentem Baltica a Moldanubikiem winna się znajdować strefa kowergencji subpolarnej („antarktycznej"). Konwergencja prądów morskich, stwarzając ostrą granicę między obszarami wód powierzchniowych o różnej temperaturze mogła stanowić dostateczną zaporę uniemożliwiającą swobodne mieszanie się faun. Wyspa Świętokrzyska, faunistycznie powiązana z kontynentem Baltica, znajdowała się zapewne na północ od konwergencji.

Posługiwanie się w rozważaniach biogeograficznych pojęciem stopnia zróżnicowania faun (diversity) nasuwa potrzebę jego jednoznacznego zdefiniowania i określenia sposobu pomiaru. Dla potrzeb niniejszego opracowania przyjąłem, za Berry *et al.* (1979), wskaźnik zróżnicowania (index of diversity) wyliczany w ten sam sposób co zawartość informacji shannonowskiej. Miarą zróżnicowania zespołu kopalnego (fossil assemblage) jest więc stopień niemożności określenia, do jakiego gatunku należy okaz losowo wzięty z próby. Wzór Shannona na zawartość informacji (I) ma postać:

$$I = -\sum_{i=1}^{n} P_i \log_2 P_i \quad \text{gdzie} \quad P_i - \text{prawdopodobieństwo poszczególnego zdarze-}$$
$$\text{nia i;}$$

po zamianie logarytmu o podstawie 2 na logarytm dziesiętny jednostką informacji zamiast bitu staje się hartley:

$$I = -c \sum_{i=1}^{n} P_i \log P_i$$

Stosując oparty na takim równaniu wskaźnik do porównywania zespołów, można pominąć współczynnik c, stosując uproszczony wzór:

$$D = -\sum_{s=1}^{n} C_s \log C_s \quad \text{gdzie} \quad C_s - \text{udział okazów poszczególnego gatunku s w}$$
$$\text{próbie (lub: stosunku liczby okazów danego gatunku do}$$
$$\text{ogólnej liczby okazów w próbie).}$$

Potrzeba ustalenia jednoznacznej, hierarchicznej klasyfikacji jednostek paleobiogeograficznych jest paląca (por. Waterhouse 1976; Kauffman and Scott 1976). Mimo znacznej liczby propozycji terminologicznych (por. Sylvester-Bradley 1971) daleko w tej dziedzinie do osiągnięcia zgodności poglądów choćby przez znaczną część badaczy. Wynika to przede wszystkim z niewielkiej stosowalności klasyfikacji opartych na zespołach lądowych do biogeografii oceanów. Ekosystemy lądowe mają z reguły ostre (dyskretne) geograficzne granice odpowiadające granicom lądów, jednoznacznemu rozdzielaniu obszarów nizinnych przez grzbiety górskie etc. Tego rodzaju zewnętrznych ograniczeń pozbawiona jest większość ekosystemów morskich. Podstawą do wytworzenia się ostrych granic mogłaby być znaczna wew-

nętrzna integracja biocenoz i związany z tym brak ciągłych przejść pomiędzy różnymi typami biocenoz. Im wyższej rangi jednostka biogeograficzna, tym jednak stopień integracji jest mniejszy. Już na poziomie ekosystemu odpowiadającego pojedynczej biocenozie stopień integracji jest nikły lub prawie żaden (Hoffman 1979). Ciągłość przestrzennych i strukturalnych przejść pomiędzy różnego typu biocenozami jest dobrze empirycznie uzasadniona (Cisne and Rabe 1977; Dzik 1979). Wyjątek stanowią biocenozy, w których koncentracja biomasy jest na tyle duża, że powoduje istotne zmiany środowiska. Tego rodzaju biocenozy mają ostre terytorialne granice. Należą tu m.in. różnego rodzaju rafy, biohermy i ławice (Dzik 1972b).

Waterhouse (1976) zaproponował hierarchiczny system klasyfikacji jednostek biogeograficznych oparty na randze charakteryzujących je jednostek taksonomicznych. Istotna wada tkwi w samym jego założeniu — niejednoznaczność i niestabilność rang taksonów pogłębia się wręcz w miarę wprowadzania wciąż nowych „filozofii" taksonomii. Można się więc obawiać o stabilność i jednoznaczność opartych na nich klasyfikacji biogeograficznych. Wydaje się, że lepszą drogę wybrali Kauffmann i Scott (1976), którzy przedstawili złożoną hierarchiczną klasyfikację jednostek biogeograficznych opartą na procentowym udziale endemicznych taksonów. Wprowadzenia tego rodzaju kwantyfikacji do opisu ordowickich jednostek paleobiogeograficznych napotyka jednak na poważne metodologiczne trudności. Stopień endemiczności jest oczywiście różny w różnych grupach organizmów (doskonałym tego przykładem może być stopień odmienności faun konodotów w stosunku do trylobitów pomiędzy Czechami i regionem bałtyckim). Nawet przy założeniu równowartościowości liczby endemitów niezależnie od grupy taksonomicznej musi to prowadzić do uzależnienia rangi jednostki biogeograficznej od stopnia opracowania taksonomicznego faun. Założenie takie nie wydaje się zresztą możliwe do przyjęcia — inny jest oczywiście sens endemiczności nektonicznego głowonoga przechodzącego w rozwoju stadium pelagicznej larwy niż np. bentonicznego ślimaka przechodzącego cały rozwój larwalny wewnątrz osłonek jajowych.

Żeby uniknąć niejednoznaczności czy arbitralnego wyboru szczegółowych kryteriów klasyfikacji przyjmuję dla potrzeb niniejszego opracowania uproszczoną klasyfikację jednostek biogeograficznych. Opieram ją nie na postulowanej wewnętrznej integracji, lecz na zewnętrznych ograniczeniach terytoriów zajmowanych przez ekosystemy, poszukując analogii z ograniczeniami terytorialnymi ekosystemów lądowych. Możliwość obiektywnego wyznaczenia granic jest w takim przypadku ograniczona przez możliwość znalezienia ostrych granic w strefach działania tych zewnętrznych czynników. Mogą to być brzegi morskie, granica szelfu, termoklina, strefa konwergencji ciepłych i zimnych prądów, zasięg wznoszenia mas wodnych dostarczających biogenów, etc. Oznacza to subtelne ale istotne przesunięcie w ujęciu definicji jednostek biogeograficznych. Nie będą one rozumiane jako wyższej rangi zespoły faun, o geograficznych granicach zależnych od taksonomicznej przynależności diagnostycznej faun, lecz jako zespoły ekosystemów (por. Kauffmann and Scott 1976). Pojęcie ekosystemu w ekologii odnosi się zazwyczaj do możliwie małego zespołu (community, assemblage, biocoenosis) wraz z jego środowiskiem abiotycznym,

który może funkcjonować jako system zamknięty pod względem przepływu informacji biologicznej (tzn. informacji funkcjonalnej, zawartej w systemach żywych i wykorzystywanej do kontrolowania przepływu energii i materii wraz z zawartą w niej informacją strukturalną). Jest to więc system o stabilnej zawartości informacji biologicznej. Zdyskredytowanie koncepcji wewnętrznie zintegrowanego, dyskretnego typu morskiej biocenozy (Hoffman 1979) każe szukać odpowiednika lądowych ekosystemów o przedstawionych właściwościach (w rodzaju lasu, jeziora etc.) na wyższym poziomie organizacji zespołów morskich. Bez zastrzeżeń można przypisać termin „ekosystem" (rozumiany jako system o prawie zamkniętym obiegu informacji biologicznej) do epikontynentalnego morza, ograniczonego przez krawędź szelfu i wybrzeża lądu oddzielające go od sąsiadnich mórz. Do tak rozumianego ekosystemu morskiego można stosować model biogeografii wyspowej McArthura i Wilsona (1963, 1967; por. Williams 1976).

Klimaksowe ekosystemy kopalne mają, w przeciwieństwie do dzisiejszych ekosystemów morskich badanych przez ekologię, istotny wymiar czasowy. Z jego istnienia wynika konieczność uwzględnienia przepływu i zmian zawartości informacji biologicznej w ekosystemach kopalnych. Zmiany te polegają na trzech rodzajach procesów biogeograficznych:

(1) ewolucji poszczególnych gatunków (dyskusyjny jest problem integracji procesów ewolucyjnych w obrębie ekosystemów, por. Boucot 1979);

(2) przemieszczaniu zespołów ogranizmów w obrębie ekosystemów (faunal shift, Jaanusson 1976);

(3) migracjach gatunków z innych ekosystemów, które mogą prowadzić w skali geologicznego czasu do zmian stanu równowagi faunistycznej (faunal equilibrium MacArthura i Wilsona 1963).

Zgodnie z przedstawionymi wyżej regułami możliwe jest stworzenie hierarchicznego systemu klasyfikacji jednostek biogeograficznych o różnym stopniu informacyjnej „nieszczelności", które mogą być zastosowane do paleobiogeografii europejskiego ordowiku. Posłużyłem się dwiema takimi jednostkami,

1. Prowincja, rozumiana jako zespół morskich biocenoz, pomiędzy którymi następuje swobodny przepływ gatunków. Ekosystemem takim było epikontynentalne morze Moldanubiku, wyspy Świętokrzyskiej czy kontynentu Baltica — dzisiejszym odpowiednikiem może być Morze Północne lub Bałtyk.

2. Państwo (realm), rozumiane jako zespół epikontynentalnych mórz rozdzielonych barierami topograficznymi (np. głębią oceaniczną) utrudniającymi ale nie uniemożliwiającymi wymianę faun. Od innych zespołów ekosystemów mórz jest ono wyodrębnione barierami hydrograficznymi podkreślającymi różnice klimatyczne i bardzo ograniczającymi migrację (np. granice kontynentów, konwergencja prądów morskich). Termin ten można więc odnieść do kontynentu Baltica wraz z wyspą Świętokrzyską i kilkoma innymi ekosystemami — dzisiejszym odpowiednikiem jest np. region subantarktyczny wyodrębniony przez konwergencję antarktyczną.

EXPLANATION OF THE PLATES 1—6

Plate 1

Abandoned iron mine at Ejpovice, Bohemia

1. View of the outcrop; arrow indicates an exposure of the Klabavian-Sarkan boundary.
2. Exposure of the uppermost part of the Klabava Formation (calcareous tuffite, shales, and mudstones) and the lowermost Šarka Formation (pelosiderite with iron oolites).

Plate 2

Svatoštěpánský rýbnik near Mýto, exposures of the Klabava Formation

1. Outer view of the locality; at bottom tuffite layer, left diabase, right (background) dark shales of the Šarka Formation. Arrow indicates abandoned quarry.
2. Wall of the abandoned quarry, indicated calcareous tuffite layer (tf) within shales.

Scalpellodus laevis Dzik, 1976, Klabava Formation, Svatoštěpánský rýbnik near Mýto, Bohemia

3. Asymmetric element with sharp posterior edge, ZPAL C.XII/11, × 100.
4. Asymmetric element ZPAL C.XII/12, × 100.

Baltoniodus bohemicus sp. n. (?), same locality

5. *Hi* element with untypically developed denticulation (?), ZPAL C.XII/20, × 100.

Plate 3

Drepanoistodus forceps (Lindström, 1955)?, Klabava Formation, Svatoštěpánský rýbnik near Mýto, Bohemia

1. Asymmetric element (drepanodiform) ZPAL C.XII/1, × 66.
2. Same type of elements ZPAL C.XII/3, × 66.
3. *Tr* element ZPAL C.XII/1a, × 66.
4. *Ne* element ZPAL C.XII/9, × 66.

Drepanodus cf. *arcuatus* Pander, 1856, same locality

5. Asymmetric element (drepanodiform) ZPAL C.XII/2, × 100.
6. *Tr*(?) element ZPAL C.XII/5, × 66.
7. *Ne*(?) element ZPAL C.XII/7, × 66.

Plate 4

Baltoniodus bohemicus sp. n., Klabava Formation, Svatoštěpánský rýbnik near Mýto, Bohemia

1. *Sp* or *oz* element ZPAL C.XII/14, × 100.
2. *Ke* element ZPAL C.XII/15, × 100.
3. *Hi* element ZPAL C.XII/19, × 100.
4. Same element type ZPAL C.XII/17, × 100.

Scalpellodus laevis Dzik, 1976, same locality

5. Twisted element ZPAL C.XII/6, *a* × 66, *b* × 1000.

Plate 5

Baltoniodus bohemicus sp. n., Klabava Formation, Svatoštěpánský rýbnik, Bohemia

1. *Tr* element ZPAL C.XII/21, × 100.
2. *Pl* element ZPAL C.XII/16, × 100.
3. *Ne* element ZPAL C.XII/18, × 100.
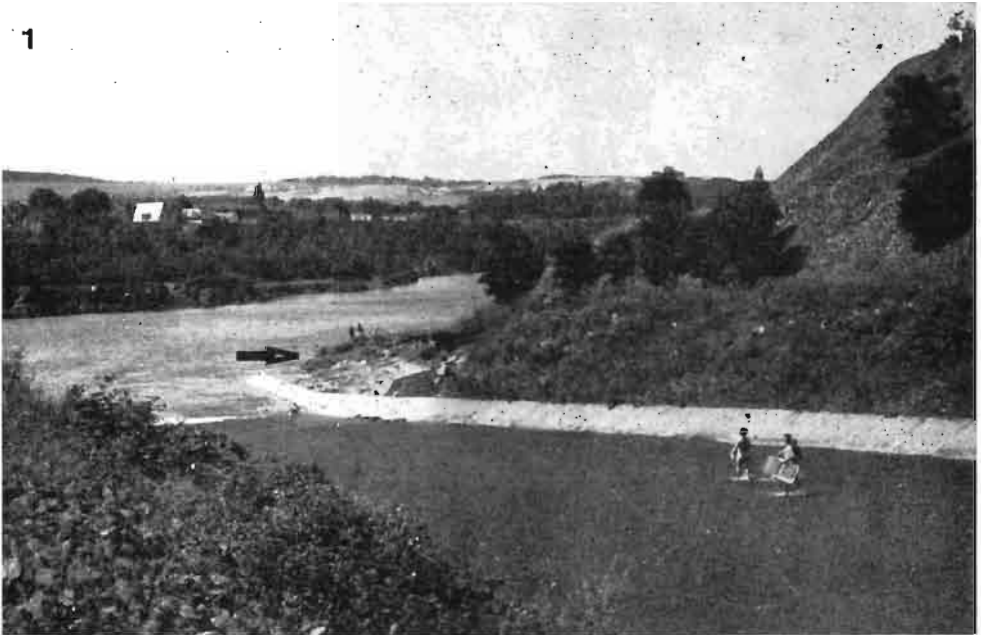4. Holotype, same element type ZPAL C.XII/12, × 100.

Oncosella sp. n.

5. Ectosomal hexactin, × 66.
6. Endosomal hexactin, × 66.
7. Bilaterally symmetrical spicule, × 66.

Plate 6

Trace fossil from the uppermost Klabava Formation, Ejpovice, Bohemia.
Scale 10 cm.

1. *Climactichnites* (?) trail on the bedding plane of red shale.
2. *Bergaueria* burrows penetrating red shale.